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# ECOLOGY

ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

OFFICIAL PUBLICATION OF THE

ECOLOGICAL SOCIETY OF AMERICA

CONTINUING THE PLANT WORLD

VOLUME III, 1922

WITH SIXTY-THREE TEXT FIGURES

PUBLISHED QUARTERLY

IN COOPERATION WITH THE ECOLOGICAL SOCIETY OF AMERICA

AT PRINCE AND LEMON STREETS, LANCASTER, PA.

BY THE

BROOKLYN BOTANIC GARDEN

BROOKLYN, N. Y.

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## ERRATA

Page 211, omit the thirteenth line from the bottom of the page, which reads "shallow margin of the lake is being slowly filled by the growth of these three."

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# ECOLOGY

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# The Journal of Ecology

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By A. G. TANSLEY

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Annual Meeting.

List of Members.

Summer Excursions, 1921.

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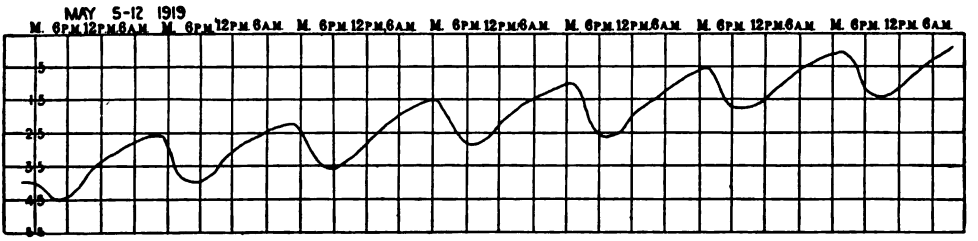


**Figure 1**

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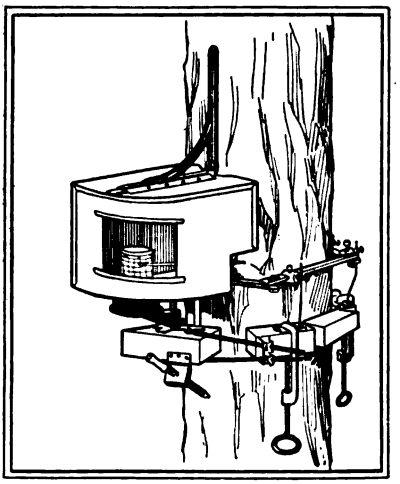

**Figure 2**

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[See **"Growth in Trees,"** Publication 307, Carnegie Institution of Washington, 1921]

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# ECOLOGY

VOL. III JANUARY, 1922 No. 1

## CITY STREET DUST AND INFECTIOUS DISEASES[1]

JACQUES W. REDWAY, F.R.G.S.

*Meteorological Laboratory, Mount Vernon, N. Y.*

The congestion of population within filthy and ill-kept quarters has created many problems concerning public health that practically are unknown in rural communities. Pollution of the air and of drinking water is responsible for a considerable proportion of the death rate in almost every part of the world; in cities, however, the death rate is materially affected by the pollution of the air from causes that are remediable.

In 1917, a year free from epidemic diseases in the United States, and therefore a fair criterion, the crude death rate varied from 8.6 per 1,000 in Seattle, to 23.1 per 1,000 in Trenton, New Jersey. Had the death rate of Trenton been reduced to that of Seattle, the saving of lives would have been about 1,900; and had the death rate of Seattle been as great as that of Trenton, the toll would have been in excess of 5,000 lives. Comparing the rate of infant mortality with that of the general rate, about three fourths of the number would have been babies under two years of age.

In New York City a change in the method of cleaning the streets, washing hard-paved streets instead of dry-sweeping them, was followed at once by a lowering of the death rate. In several western cities the abolition of dry-sweeping for sanitary methods of cleaning the streets produced similar results. There are no specific statistics whereby the deaths due to polluted air may be separated from those due to other causes, but one can not ignore the unqualified opinions of health officials whose knowledge in the matter is positive.

[1] The statistics concerning the bacteriological content of the air are mainly on the authority of the following:

WINSLOW, C.-E. A., and KLIGLER, I. J., "Quantitative Study of the Bacteria in City Dust." American Journal of Public Health [Vol. 2, No. 9].

PRUDDEN, T. MITCHELL, "Dust and its Dangers." G. P. Putnam's Sons.

KENWOOD AND PARKS, "Hygiene and Public Health." P. Blakiston's Son & Co.

Bacteriological research is not carried on in this laboratory except in an incidental and rather crude way. Microorganisms are merely a part of the dust content of the air.



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City dust is the offal of an overcrowded population—paving stuff, horse dung, ashes, garbage in every stage of putrefaction, the dismembered anatomy of insects and the refuse of humanity—all ground to fineness. When reduced to microscopic size it is ready for distribution; and the diffusion of city street dust is a striking example of perpetual motion. Street traffic is the chief factor in the creation of city street dust; the rattan broom, wind, and human footsteps are the chief agents whereby it is diffused.

Wherever air currents exist in crowded localities they carry city street dust. Air currents carry dust by means of wind pressure through cracks and crevices which water will not penetrate. In a box, within another box, within a closet of this laboratory, were some vulcanite cells that had lain undisturbed for more than two years. When an occasion for their use occurred, they were covered with a gray film of dust. A quarter-inch objective showed that the dust consisted of ash from the heater, horse dung, and a few bits of wool fiber. Meteorologists sometimes discuss the properties of still air. But still air does not exist. Air currents may be strong enough to pick up, or to carry, or to drop dust; all the time they are doing the one or the other. In this particular instance lowering temperature or increasing pressure, or both, had forced dust-laden air into the box; increasing temperature or decreasing pressure in turn had forced air out of the box but the outgoing air did not overcome the adhesion of the dust to the cells. Similar movements are going on all the time. The house is merely a box into which air is forced at one time and out of it at another. Dust that settles is apt to adhere strongly. The air that goes into it is dust-laden; the air that goes out leaves the dust behind.

In city streets the rolling dust is rarely carried more than a foot or two from the ground. This slight lift, however, is sufficient to dump it into cellars, into basements, and into the intakes of ventilating chambers. Coarse dust is rarely carried above a few hundred feet, and insects are not carried higher. Even the finest street dust is not whisked more than twelve hundred or fifteen hundred feet above ground by the wind. The danger zone, therefore, is close to the ground, so far as wind-blown dust is concerned. These statements, one must bear in mind, do not apply to the floating dust of the upper air,[2] or to the region of convection; they refer to the shell of wind-blown dust only.

Probably the greater part of the dust which gets into a building is "tracked" into it. Dust blown into the air is constantly settling, and a due proportion settles on sidewalks and approaches. This dust is ground finer and finer by scuffing feet and by attrition of other kinds. Within a very few minutes after the pupils of a city public school have marched through the corridors of the building the flying dust sometimes exceeds 80,000 par-

[2] The floating dust has been discussed in a previous paper, "The Dust of the Upper Air" in ECOLOGY, Vol. II, No. 2, pp. 104–109, for April, 1921.

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ticles per cubic inch of air. Most of this dust has been tracked into the building. The imprint of a shoe fresh from the sidewalk on a piece of black cloth leaves from several hundred to several thousand dust particles per square inch.

Large dust particles—that is, those exceeding four or five micromillimeters in dimension—are not especially harmful. They are too large to become entangled in lung tissue. Even those small enough to become entangled in the lungs, are not especially harmful unless sharp-edged, such as drill dust, or grinders' dust.

The chief menace of street dust is its biological content—the presence of the microorganisms popularly known as "germs." Years ago, Dr. T. M. Prudden carried on a series of tests on the biologic content of the air. Thereby he gave a very black eye to the commonly accepted notion that air and sunlight are positively destructive to microorganisms. The theory is true in part but the exceptions are important. The tests made by Winslow and Kligler, as well as the information gathered from many other sources show that microorganisms may survive in air and in dust from a few hours to many days. The important feature is the fact that definite knowledge concerning the why and the wherefore for the difference in the period of survival does not exist. Public safety depends on the assumption that, unless sterilized, dust of any sort possesses the possibilities of infection.

The broader knowledge that Prudden emphasized is even more definite and of greater value than the specific facts which he demonstrated. His methods involved a rare combination of simplicity and practical sense. He plated shallow dishes with culture media and exposed them under standard conditions to the air. Microorganisms that fell on a culture medium very quickly developed colonies. The remaining work was the count of the colonies.

The next step was the determination of the effect of air currents. So far as the movement of visible dust particles is concerned, air moving so slowly that it will not deflect the direction of smoke may be considered as still air. Here are the results obtained by Prudden from the five-minute exposure of plated Petri dishes 3¾ inches in diameter:

| | | |
|---|---|---|
| 1. In a private residence | 34 | colonies |
| 2. In a department store | 199 | " |
| 3. At Union Square | 214 | " |
| 4. At an entrance to Central Park | 499 | " |
| 5. At Broadway and Thirty-fifth Street | 941 | " |
| 6. Where street-sweepers were at work | 5810 | " |

The moral is obvious: A light breeze whisks comparatively few microorganisms into the air; heavy and fast-moving traffic flings up a much greater quantity. But evidently winds and busy street traffic are in the kindergarten class compared with the street-sweeper's rattan broom. Even

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granting that the totals are merely rough approximations, the ratios have real values. They indicate that dry-sweeping with its consequent cloud of dust is the chief factor in air pollution. The broom sends five times as much dust into the air as does heavy street traffic, and ten times as much as a light breeze.

Winslow and Kligler strengthened Prudden's conclusions by counting the number of microorganisms in street dust. The tests ranged from 150,000 to 145,000,000 per gram. The average was more than 20,000,000 for out-of-door dust and about 5,000,000 for indoor dust. The number is much greater in water-sprinkled than in unsprinkled streets. The statistics gathered from various other sources in American and European cities gave values which were not materially different.

What is the effect of such contamination on public health? The answer is not easy. One may readily conceive a danger that does not exist; one also may ignore a danger that does exist. As a matter of fact,, humanity has been breathing polluted air for many centuries. In general, emphasis has been placed on the presence of carbon dioxide in the air and not on the dangers arising from its dust content. The evils consequent upon an excess of carbon dioxide in the air have proved something of a bugaboo. The possibilities of infection from dust pollution, long ignored, have been shown to be real and serious. Modern sanitary science has accomplished wonders in the prevention of infectious and contagious diseases. Much still remains to be done if the death rate is to be lowered. The urban death rate has been lowered little by little until, in many instances, it is lower than that of nearby rural communities. There is, however, a tremendous difference between 6.9 per 1,000 and 23.1 per 1,000.

Most of the microorganisms found in street dust are harmless. Some, like the colon bacilli, are in the class of "suspects," still others are disease-bearing and deadly. The colon bacillus is almost universal where animals are used in street traffic. It is intestinal in origin and is abundant in the fecal discharges dropped upon streets. As a part of the content of city street dust colon bacilli do not indicate the presence of typhoid bacilli.[3] Winslow and Kligler found the ratio of colon bacilli to other microorganisms somewhat greater than 1 : 1,000; in one instance the number exceeded 60,000 per gram. Their number in indoor dust averaged about one fourth that in out-of-door dust. Redway found them in the dust of various school rooms; in a public library; and on fruit exposed for sale on a public street. In medical science they are regarded as harmless under ordinary circumstances, but at times they are virulent.

The streptococcus is sometimes found in the horse-dung content of street

[3] If found in water supplies situated at a distance from public streets colon bacilli indicate fecal contamination. In such cases the water may or may not be infected with the bacilli of typhoid.

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dust; for the greater part it is a product of human carelessness, due to the habit of promiscuous expectoration. Streptococci in street dust therefore are presumably of buccal origin. In themselves they are not regarded as harmful. If they are of buccal origin, however, they indicate the probability of pathogenic microorganisms that infest the human mouth.

Of the presence of tubercle bacilli in street dust there is no question. The research of many years, covering practically all the large cities of Europe and America, show that they are rarely absent. Although street dust moves normally from out of doors to indoors, it is probable that tubercle bacilli accumulate indoors and are carried out of doors. The statistics gathered by Winslow and Kligler show that, while only about 5 percent of the microorganisms in the dust of non-infected localities are tubercle bacilli, in infected localities the proportion is five times as great. Still further, the same authors find that, while in non-infected localities only 8 percent of the animal deaths from all causes is due to tuberculosis, in infected localities about one third died from that disease. Again granting that such values apply only to the localities in which the tests were made, the results show conclusively that infection from dust is not only possible but that it may be certain. So far as Europe and the United States are concerned, tuberculosis is not only pandemic; it is always with us; and although the death rate has been lowered, the total number of deaths therefrom has increased during a period of twenty years. And a reason therefore is not hard to find. Even if all other sources of infection be eliminated, street dust is competent to keep the disease with us. In the spread of microorganisms by means of air currents, Dr. Winslow gives first place to the "March gale." One might add that; if the velocity of an air current is doubled its capacity as a carrier of loose dust increases sixty-four-fold. Even with this capacity it is doubtful if a brisk breeze puts anything over the street sweeper's rattan broom. Either one is fully competent to account for the persistence of tuberculosis.

The microorganisms of anthrax and tetanus are spore-forming; hence theoretically the greater possibilities of infection by means of the air. As a matter of fact, evidences of infection by air contact are absent so far as available statistics are concerned. The health statistics of New York City show that, in the metropolitan district, the shaving brush is the chief source of anthrax infection. Winslow's statistics show that dust from dry hair and hides are responsible for many, if not most of the cases elsewhere.

Street dust is a very far-reaching factor in epidemiography. Whenever infectious diseases hover over a locality, the street dust there is apt to contain the microorganisms of the disease. In the vicinity of hair and hide industry, the bacilli of anthrax are usually discoverable in nearby dust. Neustaedter and Thro produced poliomyelitis from the dust of an infected sick room. Research in various parts of the United States and Europe

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shows that, at times, the pneumococcus is discoverable in dust, indoors and out of doors. The bacillus of diphtheria has also been found in street dust, but its presence seems to be rare. Cases of infection by house dust are common. The microorganism of influenza, of the bubonic plague, and of Asiatic cholera do not seem to occur in street dust. They seem to have but little resistance to dry air and dust. Evidence of the existence of the typhoid bacillus in dust seems to be doubted by some bacteriologists. There are possibilities, however. The dismembered anatomy of flies is almost always discoverable in city street dust in the localities where flies are abundant. If the flies have fed on contaminated excreta, typhoid bacilli will be found in their remains. The rest is merely a question of the resistance of the bacilli.

More and more the evidence that still, dry air has but little power to convey the germs of disease is strengthening. Moist air frequently contains microorganisms; perhaps some of them may be pathogenic, but evidence at present available does not support such a hypothesis. All the evidence so far obtainable indicates that infectious air is dust-laden air. No suspicions obtain against the upper air and its dust content so far as the communication of disease is concerned. It is not much of an exaggeration to say that all the disease-bearing dust is in the neighborhood of over-populated localities and below the 1,200-foot level of the air.

Sanitation of the air concerns its proper humification and its cleanliness. Proper humification of the air indoors is not a difficult matter. Control of its dust content is more difficult. Dust may be taken from the air, it is true; it is an interesting scientific experiment. It is likewise comparable to the use of a locomotive to carry a postage stamp from Quoddy Head to Cape Mendocino. It can be done. Prevention, however, is not only possible; it is practicable. Varnishing or oiling floors will keep the dust of indoors out of the air. And when the dust is not in the air no one is breathing it. Screening the air supplied to mechanically ventilated buildings removes the greater part of the dust; washing the air—now a practice in many public buildings—removes the rest. Washing hard-paved streets not only prevents the dust from flying into the air, but also removes it beyond the possibility of doing harm. Tarring the street which this laboratory faces reduced the flying dust about 95 percent—more rather than less. Indeed anything which eliminates the rattan broom of the street sweeper is a blessing to all humanity unfortunate enough to be within the confines of dust-laden air.

"Public health is a purchasable commodity. Within natural limits a municipality may fix its own death rate." And human life is the price which a community pays for indifference and ignorance.

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# THE ECOLOGICAL LIFE HISTORY OF CERTAIN SPECIES OF RIBES AND ITS APPLICATION TO THE CONTROL OF THE WHITE PINE BLISTER RUST

WILLIAM S. COOPER
*University of Minnesota*

This study is a portion of the outcome of one season's field work upon the ecology of the gooseberries and currants in New England and the Adirondacks, undertaken for the White Pine Blister Rust Control Office of the Bureau of Plant Industry, and published here with the permission of that organization. Since *Ribes* is recognized as the most critical point in the attempt to control the disease, a thorough investigation of the life history of the various species was determined upon; the present summer's work constitutes merely a beginning. In its prosecution a number of points developed, of scientific as well as practical importance, which seem of sufficient value to warrant publication. Aside from its intrinsic results, the work is of interest in that it indicates the close relationship that is likely to be found between plant and animal factors in the investigation of an ecological problem. It also embodies the promise of a useful field and large opportunity for a new profession, that of the "consulting ecologist".

Such a study will yield far greater results if attacked from the developmental standpoint; in fact, the conclusions here presented could hardly have been attained without the prerequisite of an adequate knowledge of the successional relations of the vegetation. The logical method of presentation is therefore to begin with an outline of those communities and successions of the region which are pertinent, and to follow this with a discussion of the rôle of *Ribes* therein. Finally, the principal applications of practical value in combating the disease will be suggested.

## I. CLIMAXES AND SUCCESSIONAL DEVELOPMENT

The area comprising New England and the Adirondacks is dominated by two forest climaxes. The Northeastern Conifer Climax, in which red spruce, *Picea rubra,* white spruce, *Picea canadensis,* and balsam fir, *Abies balsamea,* are the principal species, probably controls the northern part of Maine, and certainly the upper altitudes of the higher mountains. The Eastern Deciduous Climax dominates the remainder. This must be subdivided into a northern and a southern phase. In the former, sugar maple, *Acer saccharum,* beech, *Fagus grandifolia,* and hemlock, *Tsuga canadensis,* are the character trees, and yellow birch, *Betula lutea,* and sweet birch, *Betula lenta,* are frequently



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of importance. The region controlled by this type includes southern Maine, most of New Hampshire and Vermont excluding the higher mountains, the Berkshires in Massachusetts, and the northwestern corner of Connecticut. Characterizing the latter phase, which controls southern New England, we find in addition to the above trees, which here hold a relatively minor place, a number of species of more southern range, including chestnut, *Castanea dentata,* and several oaks and hickories. Between the two climaxes, and the two divisions of the more southern one, there are naturally wide belts of transitional character.

The two phases of the deciduous forest differ strikingly in relative abundance of *Ribes,* the northern being characterized by a larger number of species and of individuals, the southern by paucity of both. White pine, *Pinus strobus,* also, toward the saving of which the present study is a contribution, finds its principal home within the area controlled by the northern phase of the deciduous forest, and plays a successional rôle leading toward the ultimate establishment of that type. This constant and close companionship between the two host plants of the blister rust plainly indicates the field of our discussion. One is justified, however, in applying the main conclusions as to the life history of *Ribes* to the southern phase as well, and for considerable distances southward and westward.

The primary successions[1] of the region must be passed over, since their importance to our problem is slight. The secondary successions,[1] on the other hand, are extremely important, and a rather detailed analysis is essential.

It should be stated at the beginning that the virgin deciduous climax which once formed a magnificent forest cover has been almost totally destroyed since the advent of the European invaders. Only here and there, and largely in the depths of the mountains, may one find areas that can safely be accepted as primeval. The period of settlement, however, has been sufficiently long to permit the attainment in many places of a close approximation to the original conditions through redevelopment. The whole area is a hodgepodge of successional communities, representing all stages from pioneer to climax.

The initiating cause of secondary development is the total or partial removal of the forest through fire, lumbering, or clearing for agricultural use, followed by abandonment. A combination of the last two is very important. The timber is removed, and crops or orchards are planted, or the ground is devoted to pasturage. Widespread abandonment of such areas has taken place during the last century, and has been followed immediately by the initiation of secondary succession. It is hardly possible to differentiate separate lines of development. There is infinite variation depending on such

[1] Clements, F. E., "Plant Succession," p. 60, Carnegie Inst. of Washington, D. C., 1916.

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factors as degree of thoroughness of forest destruction, degree of modification of habitat by culture, proximity of seed sources of various species, subsequent disturbances. In brief and very general outline the process is as follows.

The first stage is made up of various weeds and grasses. It is quickly superseded unless the area is pastured, in which case a solid turf is ordinarily formed which may maintain itself for a long period.

The second stage comprises a number of shrubby species, which are so characteristic that they may be aptly designated "pasture shrubs." In approximate order of importance these are wild red raspberry, *Rubus idaeus aculeatissimus,* hardhack, *Spiraea tomentosa,* meadow sweet, *Spiraea latifolia,* blueberry, *Vaccinium pennsylvanicum,* juniper, *Juniperus communis,* moun-

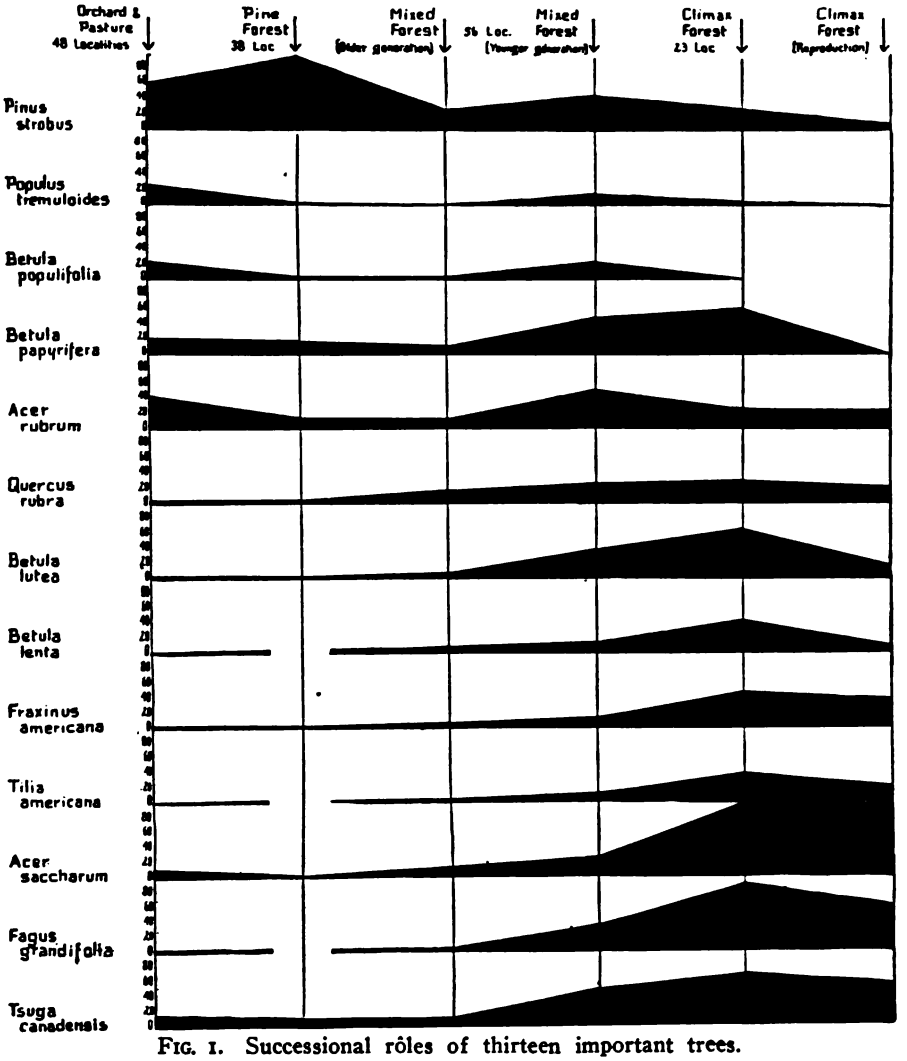


FIG. 1. Successional rôles of thirteen important trees.

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tain blackberry, *Rubus allegheniensis,* high bush blueberry, *Vaccinium corymbosum,* staghorn sumac, *Rhus typhina,* and shrubby cinquefoil, *Potentilla fruticosa.*

Of rather minor importance to the successful development as a whole, but all-important to the present subject, are three species of *Ribes: R. cynosbati, R. hirtellum,* and *R. rotundifolium,* the first universally abundant, the last two of consequence within their respective ranges.

The pasture shrubs are superseded in turn by a community embracing a number of tree species, mostly semi-xerophytic, which appear here and there among the shrubs and gradually give rise to open woodland and later to closed forest. The five most important species are white pine, aspen, *Populus tremuloides,* grey birch, *Betula populifolia,* white birch, *B. alba papyrifera,* and red maple, *Acer rubrum.* These may occur in any combination, so that a multitude of indefinable communities results. Very frequently, because of proximity of seed trees, white pine forms a practically pure stand. The seedling growth under these trees is a prophecy of the final stage. Sugar maple, beech, and hemlock are the most important species, and yellow birch, sweet birch, red oak, *Quercus rubra,* white ash, *Fraxinus americana,* and linden,

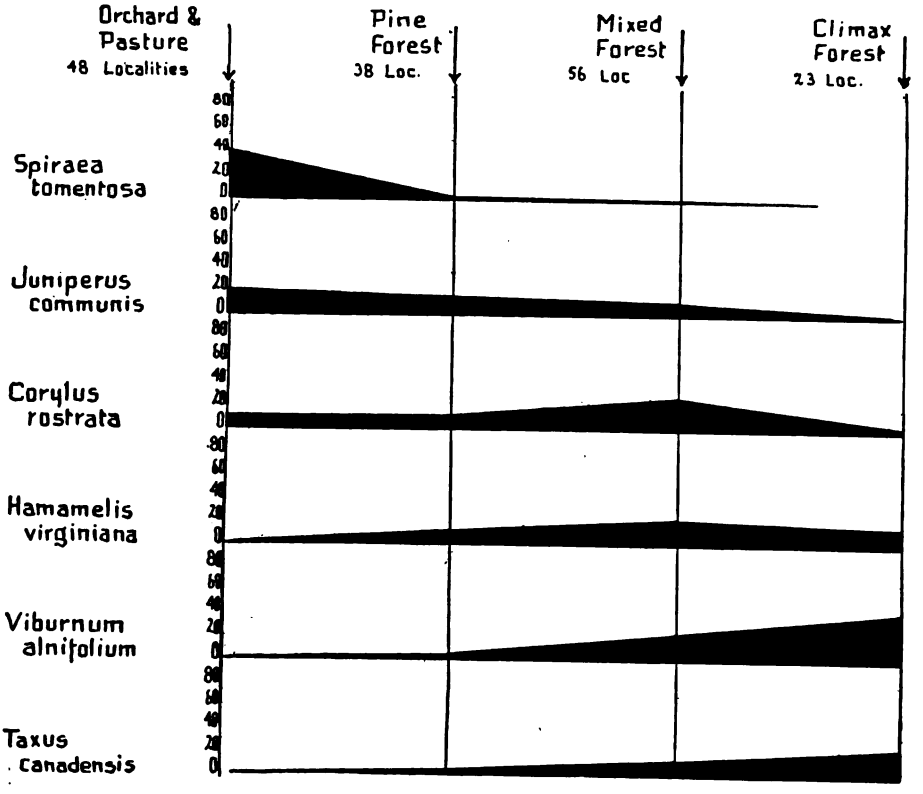


FIG. 2. Successional rôles of six important shrubs.

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*Tilia americana,* are common. The maturing of these brings back the climax, and a study of the seedling growth in areas of adult climax forest confirms the permanence of the type, with the first three species continually increasing their dominance.

Since the habitat conditions in the region are rather uniformly mesophytic, it is not surprising to find these four stages more or less telescoped, the trees beginning to come in with the pioneers, but not attaining to dominance until later.

An attempt has been made in figures 1 and 2 to represent graphically the course of the secondary succession. In figure 1 the successional rôles of thirteen important trees are shown by indicating the percentage of the total number of localities of each stage in which the species was found to be present. The method is necessarily imperfect, since it expresses merely occurrence and gives no indication of relative abundance. The open pioneer stages have been grouped under the heading "orchard-pasture". The pine forest stage is an alternative which may be omitted, as the course of development frequently passes directly into the "mixed forest" community, which includes the large number of penultimate groupings which defy logical analysis. The climax character of sugar maple, beech, and hemlock is very evident. The reproduction beneath the trees of the climax has been added to suggest the future history. Figure 2 indicates in the same manner the successional rôles of six important shrubs: two pioneer, two intermediate, and two climax.

## II. The Rôle of Ribes in Successional Development

*a. Occurrence in Various Stages of the Secondary Succession.*—The species of importance are mainly the gooseberries: *Ribes cynosbati, R. hirtellum, and R. rotundifolium.* These undoubtedly differ in preferred habitat, but not to an important degree, and my data are not sufficient to warrant separate treatment. Figure 3, in which records of the three species are combined, shows that the gooseberries occur most commonly in the orchard and pasture communities, and that they here bear most fruit and are most generally infected; that they are less common, with less fruit and infection in the mixed woodland; and least in number and infection in the climax forest. Here again we have records of occurrence only, with no indication of abundance. The descriptive field notes, however, supplement the statistical data in a very satisfactory way. They show that the plants of the pastures and orchards are almost always large, bushy, heavily fruiting, heavily infected, and that those of the mixed woodland are slender, weak, with little fruit, and moderately infected. The figures for the climax forest need some special words of explanation. The list includes a few localities that are undoubtedly primeval, together with a much larger number showing approximation to original condition through redevelopment. The eight occurrences of *Ribes*

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in the climax forest are unimportant, and almost entirely in openings of various kinds. The two occurrences of fruit are noted thus: "one *Ribes lacustre* beside main stream, fruiting abundantly"; "one berry". The two cases of infection were slight. Thus, if relative importance of record could be expressed in the figure, the rise of the curve of fruiting to the climax would be eliminated and the downward trend of the infection curve intensified, thus bringing the results into full consistency.

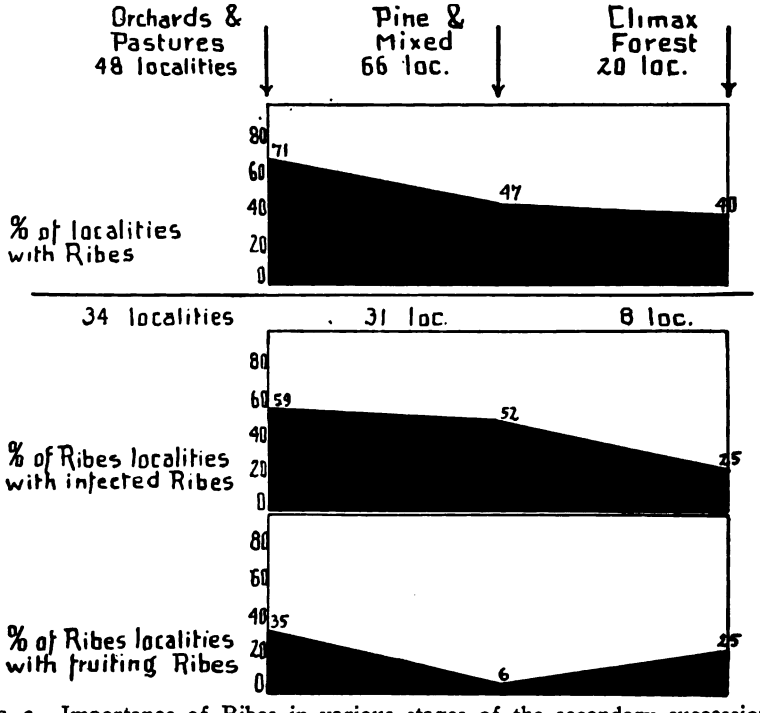


FIG. 3. Importance of Ribes in various stages of the secondary succession; relation of infection and fruiting to successional stage.

In a comparative study of leaf area as affected by environment, light being specially considered, Mr. Philip Brierley, my field assistant, discovered that in unit time (one season's growth) the gooseberries in the open pioneer stages of the succession produced an area of leaf surface 22 percent greater than those in the closed forest, the difference being due to greater average shoot length and consequent larger number of leaves, which more than balanced the smaller average size of leaf.

We conclude, therefore, that the gooseberries are abundant, large, and healthy in the early stages of the succession, fruiting heavily and also heavily infected; that they decrease in number and robustness as the succession advances, and in amount of fruit and infection as well; and that in the mature

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climax forest they seem near to elimination, those remaining bearing practically no fruit and almost no infection. The explanation of these facts is next in order.

*b. Modes of Dissemination.*—There are four possibilities: wind, gravity, running water, animals. The first may be dismissed. Gravity may carry the berries for short distances where slopes are steep and thus bring about occasional establishment in unusual situations. Running water may do likewise, and this doubtless accounts for the rather frequent occurrence of bushes along stream courses in deep forest. Both these factors are relatively unimportant beside the last. The two groups of animals that are effective disseminators are certain birds, and chipmunks and other small rodents. I have been unable to obtain sufficient data to warrant extended discussion of the latter.

The evidence as to birds is fairly satisfactory. The simplest method of approach is first of all to determine upon a list of the habitual fruit eaters, which has been done with the aid of all available literature, the result being given in Table I. The next step is to classify these twenty-six species according to habitat. Adams[2] has shown that there is a definite ecological succession of birds. Certain groups of species, or bird communities, are related to certain plant communities, and as the latter replace one another in the course of successional development, the bird communities change likewise. The bird population of the climax forest is thus very different from that which was associated with the temporary pasture stage which preceded its establishment, and which may very likely be found in some nearby locality where vegetational development has not progressed so far. Allowance must be made for the greater mobility of the bird population, resulting in less definiteness than is to be found in the plant communities. In the secondary successions of the New England region the greatest change in bird life accompanies the transition from open pasture to mixed woodland; the change from that to climax being much less significant so far as birds are concerned. For brief discussion, therefore, we may fairly contrast the birds of the open with the birds of the forest. An intermediate class must be inserted to provide for those species that are not strictly confined to either community. In the following table the general classification has been made from the literature, especially the publications of the Biological Survey. That organization has also kindly furnished the results of all stomach analyses in which evidence of *Ribes* was obtained, and these data have been added, the denominator representing the total number of analyses, the numerator the number containing *Ribes;* with the resulting percentage.

[2] Adams, C. C., "The Ecological Succession of Birds," The Auk 25: 109–153, 1908.

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TABLE I. *The relation of birds to the dissemination of Ribes*
*Showing number of analyses containing Ribes seeds, total analyses, and resulting percentage with Ribes seeds*

*With Ribes Records*

| OPEN | | UNRESTRICTED | | FOREST | |
|---|---|---|---|---|---|
| Catbird, 20/677..... | 3.00% | Wood Thrush, 1/173.. | .58% | Hermit Thrush, 3/639..... | .47% |
| Chewink, 10/683..... | 1.47 | Red-headed Woodpecker, 3/534. | .56 | Ruffed Grouse, 1/250..... | .43 |
| Blue Jay, 9/678..... | 1.32 | Red-eyed Vireo, 1/654..... | .15 | Olive-backed Thrush, 1/476..... | .21 |
| Cedar Waxwing, 2/210... | .95 | | | | |
| Robin, 13/1392..... | .93 | | | | |
| Brown Thrasher, 6/660... | .91 | | | | |
| Bluebird. 2/859..... | .23 | | | | |
| Crow, 4/2215..... | .18 | | | | |
| Flicker, 1/718..... | .14 | | | | |
| Kingbird, 1/711..... | .14 | | | | |

*No Ribes Records*

| | | |
|---|---|---|
| Chipping Sparrow | Rose-breasted Grosbeak | Purple Finch |
| Song Sparrow | Baltimore Oriole | Wilson's Thrush |
| Warbling Vireo | Yellow-bellied Sapsucker | |
| | Downy Woodpecker | |
| | Hairy Woodpecker | |

From this table we draw the following facts: The birds of the forest, almost without exception, do not eat fruit. Of the birds of the open, many eat fruit more or less, and of the thirteen listed, ten have records of *Ribes* to their credit. Of the eight classified as unrestricted, only three have *Ribes* records.

The third step relates to the comparative abundance of the various fruit eaters. Nearly all the very abundant birds fall in the "open" column; all but two of these are exceedingly common. Only two or three, at the most, of the "unrestricted" species can fairly be classed with the majority of the first group as to abundance. The remainder of the "unrestricted" birds and the forest birds are relatively infrequent.

We conclude, therefore, that the fruit-eating birds of the open, which do not frequent the forest, are numerous in species and especially abundant in individuals; that most of them have *Ribes* records, including all the high percentages; and that as a class they are very effective as planters of *Ribes*. The birds which frequent both open country and forest are fairly numerous in species, but are nearly all relatively uncommon; few have *Ribes* records and all the percentages are low. Seeding of *Ribes* in the forest due to this

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class may occur, but must be of very slight importance. The same may be said of the species exclusively of the forest. The abundance of gooseberries in pastures and cleared grounds in general hardly needs further explanation. Additional evidence of incidental nature is found in the remarkably consistent occurrence of gooseberry bushes close to ancient apple trees in deserted orchards and beside isolated pasture trees; and in the occasional bushes growing high in crotches.

*c. Subsequent History.*—We have seen that nearly all of the seeding of gooseberries, from extraneous sources, is due to certain fruit-eating birds, and that it takes place almost entirely in the early stages of the secondary successions, while the vegetation is in the pasture, old orchard, or some other open sort of condition. The subsequent vegetational history, whatever the invading tree species, is one of increasing density and shade, and the fruit-eating birds are gradually eliminated and the insect-eating species of the forest take their place. There is thus no further opportunity for the seeding in of *Ribes* in any quantity from extraneous sources. An occasional plant may become established through the agency of some stray pasture bird, or forest bird that has found gooseberries to its taste, or through water or gravity. All these combined can not bring in *Ribes* in appreciable numbers. Practically all of the gooseberries found in closed forest (and they are sometimes rather abundant in such places) must then be either original bushes surviving from open conditions or their direct progeny. There is abundant evidence that gooseberries may be long-lived even under relatively unfavorable conditions. Their persistence in deep forest is thus not surprising. As the shade increases in the course of successional development, the *Ribes* bushes take on the characteristic forest form of single weak spindling shoots, often prostrate, instead of the sturdy clump characteristic of the open pasture. Moisture and light conditions now favor the process of layering, and the plant lives on from year to year, dying off behind and continually renewing itself by producing fresh shoots. In this way it may persist for many years, but apparently is ultimately doomed to extinction.

It has been shown that the abundance of fruiting decreases strikingly with increase of shade, so that in the climax forest it is rare to find any fruit at all. Thus the plant must fail to perpetuate itself, and given time and freedom from disturbing agencies, *Ribes* will ultimately practically disappear from the forest community.

## III. Practical Applications

1. The study shows that no plant community may be consistently and safely disregarded in the search for *Ribes*. The only possibility is the beech-maple-hemlock climax, and this is so limited in extent in the region where eradication is likely to be practiced that its immunity, even if true, is of little

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practical significance. The great mass of the country is either favorable for *Ribes* introduction at the present time or may support *Ribes* holding over from former conditions.

2. It seems possible to prophesy with reasonable certainty whether a given tract, once made free of *Ribes,* will remain so indefinitely, or will have to be watched carefully from year to year. In general, closed forest, once thoroughly cleaned of gooseberries, can be safely disregarded in the future, since there are no effective agencies that will renew the species from without. Any individuals that do become established will develop a minimum of infection and of fruit in such places. Open pastures, old orchards, thickets, and similar places must be carefully watched for new arrivals, since the agents of dissemination are continually active therein, and infection is likely to be heavy. Thorough care of such critical places will also operate to prevent accidental introduction of seed into nearby closed forest.

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# THE SUNFLOWER AND ITS INSECT VISITORS

CHARLES ROBERTSON

*Carlinville, Illinois*

The sunflower, *Helianthus,* belongs to about the largest, most uniform, and most commonplace of the natural families. Compared with the Compositae in general (3 and 5 in table), it shows a higher percentage of bee species and a higher percentage of bee visits, as well as a higher percentage of species of Lepidoptera, and a lower percentage of other insects. This is because the corolla tubes are deeper than in the average Compositae. It resembles rosin-weed, *Silphium* (4 in table). Of the 655 species found on Compositae at Carlinville 21.8 percent occur on *Helianthus.* It forms 9.4 percent of the local Compositae and shows 8.1 percent of the insect visits.

TABLE. *Visits of insects to flowers of* COMPOSITAE, *by species of insects and number of visits*

| List | | Bees alone | | Bees and other insects | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Long-tongued bees | Short-tongued bees | Bees | Dipt. | Hym. | Lep. | Col. Hem. | Total number |
| | | In percentages of all insects | | Percent | | | | | |
| 1. Carlinville, 1894, 1898 | Species | 37.1 | 16.4 | 53.6 | 18.5 | 4.1 | 18.5 | 5.1 | 97 |
| | Visits | 40.9 | 16.1 | 57.1 | 21.7 | 2.4 | 14.4 | 4.3 | 161 |
| 2. 23 other localities | Species | 45.3 | 25.3 | 70.6 | 6.6 | ..... | 20.0 | 2.6 | 75 |
| | Visits | 47.9 | 25.0 | 72.9 | 5.2 | ..... | 18.7 | 1.0 | 96 |
| 3. Present list | Species | 34.9 | 18.1 | 53.1 | 19.5 | 6.9 | 13.9 | 6.1 | 143 |
| | Visits | 42.1 | 20.0 | 62.1 | 18.1 | 3.7 | 10.0 | 5.8 | 320 |
| 4. *Silphium* | Species | 37.3 | 13.3 | 50.6 | 18.6 | 4.0 | 26.6 | ..... | 75 |
| | Visits | 51.1 | 12.4 | 63.5 | 16.2 | 3.1 | 17.0 | ..... | 129 |
| 5. Compositae | Species | 14.3 | 15.1 | 29.4 | 30.3 | 23.8 | 10.2 11.6 | 6.1 | 655 |
| | Visits | 23.4 | 17.3 | 40.7 | 27.3 | 17.5 | | 2.7 | 3,905 |
| 6. *H. annuus* and *divaricatus* | Species | 51.3 | 16.2 | 67.5 | 10.8 | 2.7 | 13.5 12.2 | 5.4 | 37 |
| | Visits | 55.1 | 14.2 | 69.3 | 10.2 | 2.0 | 2.7 | 6.1 | 49 |
| | Individuals | 71.9 | 14.1 | 86.0 | 8.3 | 0.2 | 11.1 | 2.5 | 467 |
| 7. *H. annuus* | ..... | 52.7 | 22.2 | 75.0 | 8.3 | ..... | 10.4 | 5.5 | 36 |
| 7 wild species | ..... | 43.6 | 19.7 | 63.4 | 18.6 | 4.4 | ..... | 2.9 | 268 |
| 8. Alfken's list | Species | 92.8 | 0.0 | 92.8 | ..... | ..... | | 7.1 | 14 |
| Others' lists | Species | 28.5 | 4.7 | 33.3 | 47.6 | ..... | 4.7 | 14.2 | 21 |
| | Visits | 41.6 | 2.7 | 44.4 | 44.4 | ..... | 2.7 | 8.3 | 36 |

The tubes are about 6 mm. deep. Since small insects can thrust their heads a little way into the tubes, and since nectar rises in the tubes, we may



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expect to find on the flowers almost any anthophilous insects with tongues 4 or 5 mm. long and upwards. *Helianthus* is therefore adapted to rather long-tongued bees and other insects. The miscellaneous character of the long-tongued visitors is shown by the following percentages of the local insects, the second figure being for species flying while *Helianthus* is in bloom: Bombidae, 88.8, 88.8; Megachilini, 50.0, 53.3; *Coelioxys*, 83.3, 83.3; *Triepeolus*, 81.8, 81.8; *Melissodes*, 52.3, 55.5; or in general: Megachilinae, 59.0, 61.9; Epeolidae, 66.6, 75.5; total long-tongued bees, 35.6, 53.6—Halictidae (ex. Sphecodini), 30.2, 34.2; Panurgidae, 37.5, 37.5; Andrenidae, 5.8, 33.3; total short-tongued bees, 18.0, 28.1—total bees, 26.6, 40.9—Rhopalocera, 25.3, 29.3—Bombyliidae, 45.4, 55.5.

According to my present list the following 23 are the most regular visitors at Carlinville, occurring at least on four out of eight species:

**Long-tongued bees** (11:67)—BOMBIDAE: *Bombias separatus* 6, *Bombus americanorum* 7; MEGACHILIDAE: *Megachile brevis* 5, *Sayapis sayi* 5; *Xanthosarus latimanus* 7; EPEOLIDAE: *Triepeolus concavus* 7, *T. cressonii* 4; EUCERIDAE: *Epimelissodes obliqua* 8, *Melissodes agilis* 7, *M. coloradensis* 6, *M. trinodis* 5.

**Short-tongued bees** (5:26)—HALICTIDAE: *Chloralictus pilosus* 5, *Odontalictus ligatus* 6; DUFOUREIDAE: *Halictoides marginatus* 4; ANDRENIDAE: *Pterandrena helianthi* 5, *P. pulchella* 6.

**Diptera** (5:27)—SYRPHIDAE: *Eristalis transversus* 6; BOMBYLIIDAE: *Anthrax halcyon* 4, *Exoprosopa decora* 4, *Sparnopolius fulvus* 7, *Systoechus vulgaris* 6.

**Lepidoptera** (1:5)—PIERIDAE: *Eurymus philodice* 5.

**Coleoptera** (1:5)—LAMPYRIDAE: *Chauliognathus pennsylvanicus* 5. The list shows 17.4 percent of the legitimate visitors making 42.7 percent of the legitimate visits.

My local lists[1] show 161 visits made by 97 species of insects (1 in table). The present list shows 143 species making 320 visits (3 in table). Six local species have been noted by other observers, so that 149 local insects have been found on *Helianthus*. Lists of visitors from other localities might differ for the following reasons:

1. The observers did not take the trouble to note all of the insects occurring or to make a careful list.

2. The plants may have formed poor patches not surrounded by the original flora and not exposed to the original insect fauna. Cultivated species like *H. annuus* are likely to be very unfavorably situated in this regard. It is about as futile to observe such plants as to trifle with those more favorably placed. Data made under such conditions belong to pseudecology. *H. annuus* growing in my yard within about a quarter of a mile of wild species,

[1] "Flowers and Insects—Rosaceae and Compositae," Trans. Acad. Sci. St. Louis **6**: 469–71, 1894, and "Flowers and Insects," XVIII, Bot. Gaz. **25**: 244–5, 1898.

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and observed on 29 days, showed too many bees, Coleoptera, and Hemiptera and was short on Diptera and other Hymenoptera (7 in table, based on legitimate visits). On the 7 wild species Diptera always show at least 16.6 percent of the visitors.

3. The plants may have been exposed to quite a different insect fauna. Differences in species and genera are to be expected, but are rather trivial.

Since the 1894, 1898 lists were published observations by 13 persons in 23 different localities have been recorded. Of the visitors which they mention 26.6 percent have been observed at Carlinville. Their fragmentary nature is shown by several facts. They give 75 visitors and 96 visits, an average of 4.1 visits for each locality and 7.3 for each person (2), while the 1894, 1898 lists give 97 visitors and 161 visits (1). In 35.8 percent of the species and 35.7 percent of the visits the sexes of the bees are not given. When the sexes are given the host bees are indicated as collecting pollen in only 12.1 percent of the species and 9.0 percent of the visits. The Carlinville list shows them collecting pollen in 57.5 percent of the species (71.9 in present list) and 47.8 percent (60.6 in present list) of the visits: long-tongued bees 67.7 percent of the species and 45.5 percent of the visits, short-tongued bees 73.0 percent of the species and 84.3 percent of the visits. These lists exaggerate the importance of bees and Heterocera and underestimate the importance of Rhopalocera and Diptera.

As data of anthecology collectors' notes are likely to prove worthless, because the collector naturally looks out for particular kinds of insects and is not interested in ascertaining what kinds of insects occur on the flowers, or their relative frequency. As entomological data they are equally worthless, because collectors select flowers on which the desired insects are most likely to occur, and they almost invariably fail to note what the insects are after.

The difference between anthecological data and collectors' notes is pretty well shown by the *Helianthus* lists in Knuth's Blütenbiologie. Alfken's list shows bees 92.8 percent, while the lists of Müller, Knuth, and Loew show: bees species 33.3 percent, visits 44.4; flies species 47.6, visits 44.4 (8 in table). These authors found flies on 7 out of 9 species, while Alfken records none.

As entomological data the differences in the two sets are just as striking. To the flower visits of Diptera, Alfken's list contributes nothing, while the other lists contribute just as many Diptera visits as bee visits.

It is interesting to note that Knuth, in his handbook "based upon Hermann Müller's work," prints Müller's lists for the third time, introduces collectors' notes which ignore Müller's method, and suppresses American lists which follow it. Knuth gives fragmentary observations made in Europe where *Helianthus* is cultivated and suppresses pretty extended lists made in America where it is indigenous. He suppresses French and Italian insect-collectors' notes on the ground that it would require too much labor to collate

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them, but he suppresses American anthecological lists evidently for a different reason.

Sometimes *Chauliognathus pennsylvanicus* fairly swarms on the flowers of *Helianthus* and at other times *Sparnopolius fulvus* is just as abundant, but these cases do not indicate the usual conditions. It would be a mistake for a casual observer to infer that such a condition was regular for any locality.

In the long list of miscellaneous visitors *Halictoides marginatus,* which gets its pollen exclusively from the flowers, is the only one entitled to be designated as a *Helianthus* insect.

*Apis mellifera* is the most regular visitor recorded in different lists. Of 196 visits observed at Carlinville, 28.5 percent are to Compositae. Of 105 visits observed after June, 44.7 percent are to Compositae. Of 153 individuals taken in my yard on *H. annuus,* in 1917, *Apis* showed 40.5 percent. Of 467 individuals (6 in table) taken on *H. annuus* and *divaricatus* it showed 14.1 percent.

*Megachile* (1894, 1898) forms 11.3 percent of the species and makes 8.0 percent of the visits. Of the local species flying when *Helianthus* is in bloom these lists show 53.3 percent. My present list shows 59.0 percent of the species, 61.9 of those flying in the *Helianthus* season.

The statement that the bumblebees occurring on *Helianthus* are principally males is not supported by any observations. Visits of bumblebees (1894, 1898) show: ♂ 52.3 percent, ♀ 38.0; and in the present list: ♂ 47.2, ♀ 44.4. Of 94 individuals taken on *H. annuus* 74.4 percent were workers and 25.5 males. The workers, which are after nectar and pollen, are more apt to occur than the males which are after nectar. The occurrence of the male establishes a presumption that the worker of the same species also occurs on the flowers. Of 261 visits of bumblebees to Compositae, observed only after June, 48.6 percent were made by the workers and only 40.2 by the males.

That there is a general absence of butterflies as sunflower visitors is not supported by any reliable observations. Butterflies (1894, 1898) are 15.4 percent of the species, making 12.6 percent of the visits. Of local species 25.6 percent were found on *Helianthus,* 37.3 percent of those flying in the blooming season. *Helianthus* will probably show 25 percent of the Rhopalocera in any locality where it is indigenous. These flowers belong to a class particularly preferred by butterflies, general social flowers with deep-seated nectar, Mas, as shown in the following 1,407 visits observed at Carlinville:

| | Non-social | | Social | | | Total |
|---|---|---|---|---|---|---|
| | Ma | Mi | Mas | Mis | Pol | |
| Flowers observed | 30.1 | 24.2 | 18.8 | 21.5 | 5.2 | 441 |
| Rhopalocera visits | 16.2 | 10.0 | 42.5 | 22.6 | 8.5 | 1407 |

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Mas forms 18.8 percent of the flowers observed and receives 42.5 percent of the butterfly visits.

The Heterocera (1894, 1898) show 3.0 percent of the species and 1.8 percent of the visits. For 143 species and 320 visits the percentages are 2.0 and 1.2. A correct list is not likely to show much difference in any locality. They are not likely to occur in abundance at the time of day when *Helianthus* pollination is usually effected.

Of local families the Megachilidae is the only one showing over 10 percent of the species (10.5 percent). The Euceridae, Megachilidae, and Halictidae show the following percentages of the visits: 13.1, 10.6, 10.3. Of 467 individuals (6 in table) taken on the flowers the following showed these percentages: *Bombus americanorum* 27.4, *Apis mellifera* 14.1, *Odontalictus ligatus* 10.9, *Melissodes agilis* 10.4; Bombidae 37.6, Euceridae 17.9, Halictidae 13.7.

When flowers like *Helianthus,* adapted to miscellaneous long-tongued insects and blooming from July 6 to October 15, show 143 species observed by one person in one locality, it is easy to see that the number actually occurring might be quite different from what this one observer saw. It is also easy to see that the flowers ought to show more than an average of 4.1 in 23 other localities. If these 4.1 visitors are made a basis of generalization, the conclusion may be drawn that *Helianthus* is visited by different kinds of insects in different localities. Unless the flowers were observed under normal conditions about every other day during the season and showed at least about 100 visitors, it would hardly be reasonable to accept the conclusion that the visitors are essentially different from those observed at Carlinville. Even then it ought to be shown that the composition of the insect fauna is different.

A final result of observations in different indigenous localities would be that, *of insects flying in the blooming time, Helianthus* would show about 53.6 percent of the long-tongued bees, 28.1 of the short-tongued bees, 29.3 of the Rhopalocera, and 55.5 of the Bombyliidae—sooner or later about all of the North American long-tongued anthophilous insects.

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# THE FAUNA OF AN ACID STREAM[1]

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## INTRODUCTION AND METHODS

Although it is well known that many streams of our country, including especially the Monongahela and even the Ohio, are becoming acid due to industrial wastes, so far as I know few, if any, studies have yet been made on the biology of a naturally acid stream or of a stream in the early stages of becoming acid. Such a stream is the Big Muddy River of southern Illinois. The author had the opportunity of making two trips to this river and of collecting some data on it while engaged in a study of stream pollution for the Illinois State Water Survey. Although these trips were of a purely preliminary nature, yet, inasmuch as the work has not been continued, and since some of the data are of considerable interest, it has seemed advisable to make the results available to those interested in the same or similar problems.

An essential feature of such a study is that all chemical determinations be made in the field. It is as impossible to determine the hydrogen-ion concentration of a river from samples of water transferred to the laboratory as it would be to determine its temperature. The author used the buffer solutions of Clark and Lubbs (1) sealed in non-soluble test tubes with 0.2 c.c. of indicator solution. The water to be tested was added to a corresponding amount of indicator in a similar test tube and comparison was made immediately in the field. The color standards were freshly prepared before leaving the laboratory for each trip and were checked with freshly prepared standards immediately upon returning. The accuracy of this method is about $\pm$ $P_H$ 0.1. Without exception, water samples were taken below the surface and from midstream.

## DATA

Most of the streams of Illinois are basic. Water from midstream of those upon which the author has made observation, the Mississippi, Illinois, Kaskaskia, Embarras, Vermillion, and Sangamon, showed alkalinities varying from $P_H$ 7.4 to $P_H$ 8.5 or higher. The water of the Big Muddy varied between $P_H$ 5.8 and $P_H$ 7.1.

The larger part of the Big Muddy River and its tributaries lies in the great coal fields of southern Illinois (fig. 1), and in rainy weather receives

[1] Presented before the Ecological Society of America at its meeting in Chicago in December 1920.



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water from at least three distinct sources; (1) rain water and surface run off, probably neutral to weakly basic, (2) ground waters, frequently acid, and (3) waters pumped from the mines, usually strongly acid. During the dry season the only source of water is the ground water.

Two trips were made to the Big Muddy River. At the time of the first, February 27 to March 1, 1919, the stream had but recently returned to its banks following heavy rains, and was still much swollen. Two weeks previously the bottoms had been inundated and large amounts of highly mineral-

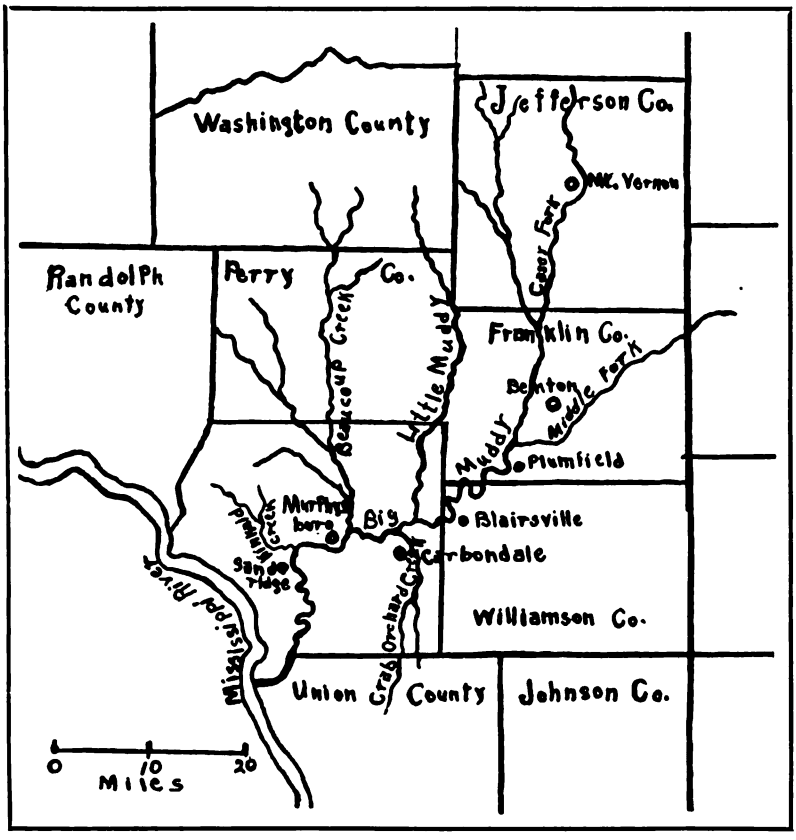


FIG. 1. Map of southeastern Illinois showing the Big Muddy River and its tributaries.

ized mine waters were still being received. The acidity of the water samples taken ranged from $P_H$ 6.2 to $P_H$ 5.8. Upon standing a few minutes these values changed from $P_H$ 6.6 to $P_H$ 6.4, although the water did not become neutral after twelve hours' exposure to the air, showing that the acidity was not due, or was due only in part, to carbonic acid. The second trip was taken by canoe during the dry season, July 29 to August 22, 1919, starting in the upper part of the river (opposite Benton), where it was so shallow that the canoe containing the apparatus had to be dragged most of the time, and

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continuing to a point shortly above the river's mouth and below the entrance of the last important tributary. At this time, except locally, the water was weakly acid to neutral, $P_H$ 6.8 to $P_H$ 7.1 or 7.2, the acidity being higher in the upper part of the stream, in the heart of the coal country where even the springs are acid, and decreasing toward the mouth where the tributary ground waters become basic.

It is the finding of these acid springs which is the basis for calling the Big Muddy a "Naturally Acid Stream," admitting, however, that the acidity is, at times, greatly increased by human agencies. These springs bubbled or seeped up through a layer of fine white sand at a temperature much below that of the river, which would indicate a deep origin; thus spring No. 1 had a temperature of 14.6 degrees Centigrade on a hot August afternoon when the temperature of the river was about ten degrees higher. Although the water itself was clear and sparkling, the sand around was stained a bright red with iron oxide precipitated upon contact with air. The hydrogen-ion concentration of the water was about $P_H$ 5.5 and was not materially altered by exposure to air for two hours with frequent shaking, showing that the acidity was not due to carbonic acid. The high acidity of mine waters is usually due to sulfurous acid produced by the oxidation of iron pyrites present in coal. Although the bottle of water from this spring collected for mineral analysis was unfortunately broken in transit to the laboratory, the precipitate of iron oxide around the spring, the inky appearance of tea and coffee made from the water, and the characteristic taste, all point to a similar source of acidity.

Table 1 gives the hydrogen-ion concentrations and methyl orange titrations (alkalinity as ppm. $CaCO_3$) characteristic of various parts of the stream. In this table distances, where given, were estimated as following the course of the stream.

It is probably not without significance to the inhabitants of the stream that the highest acidities occurred at low temperatures, and that during the heat of the summer the water was almost neutral, since it has been repeatedly shown (Gail, 2; Powers, 4; Stickney, unpublished) that the effects of acids or toxic substances increase rapidly with an increase in temperature.

The biological survey was made during the summer trip. The stagnant character of the stream makes it especially favorable for abundant algal growths, which do not appear to be in the least inhibited by the acidity. The felt-like masses of oscillaria which covered the surface and bottom of the pools were the heaviest the author has ever seen. Thick scums of euglena were common, while desmids, tabellarian diatoms, and colonial phytoflagellates were also abundant. Of the zooplankton forms the most characteristic were the ostracoda, copepoda, and bryozoon statoblasts (*Pectinatella*).

The bottom fauna of a stream is always of interest because its forms, being unable to migrate with a changing environment, are limited by the

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TABLE I. *Results of field tests on the water of the Big Muddy River*

| Locality | Date | Temp. degrees C. | Alkalinity as ppm. $CaCO_3$ | PH |
|---|---|---|---|---|
| 1. Casey Fork at Mt. Vernon | Feb. 27 | 3 | 43 | 6.9 |
| | July 29 | 29.6 | 57 | 7 |
| 2. Big Muddy near Benton | Feb. 28 | 7 | 19 | 6.2 |
| | July 30 | 28.7 | 78 | 7 |
| 3. Three miles below Benton River, | Aug. 1 | 24 | 96 | 6.8 |
| Spring No. 1 | Aug. 1 | 14.6 | 43 | 5.5 |
| 4. Ten miles below Benton River, | Aug. 2 | 24 | 90 | 6.8 |
| Spring No. 2 | Aug. 2 | 16.6 | 58 | 5.6 |
| 5. Thirteen miles below Benton River, | Aug. 13 | 25 | 82 | 7.1 |
| Spring No. 3 | Aug. 13 | 18 | 58 | 5.6 |
| 6. Above Junction of Middle Fork | Aug. 14 | 25 | 79 | 7.0 |
| 7. Middle Fork | Feb. 28 | 5 | 18 | 5.9 |
| | Aug. 14 | 25 | 90 | 7.1 |
| 8. Plumfield | Aug. 14 | 25 | 78 | 7.0 |
| 9. Blairsville River, Spring No. 4 | Aug. 18 | 26 | 50 | 7.0 |
| | Aug. 18 | 22 | 428 | 7.6 |
| 10. Above junction of Little Muddy | Aug. 19 | 22.5 | 124 | 7.2 |
| 11. Little Muddy | Aug. 19 | 22 | 100 | 6.8 |
| 12. Below Little Muddy | Aug. 19 | 22 | 115 | 7.1 |
| 13. *Carbondale below Crab-Orchard Creek | Mch. 1 | 5 | 15 | 5.8 |
| Surface Sample | Aug. 20 | 24 | 90 | 6.8 |
| Bottom Sample | Aug. 20 | 24 | 90 | 6.6 |
| 14. Spring Fed Creek, 6 miles below Carbondale | Aug. 20 | 20 | 516 | 8.0 |
| 15. Above Beaucoup Creek | | | | |
| Surface | Aug. 20 | 24 | 140 | 7.1 |
| Bottom | Aug. 20 | 24 | 142 | 7.0 |
| 16. Beaucoup Creek | Aug. 20 | 24 | 146 | 7.1 |
| 17. Murphysboro | Mch. 1 | 5.2 | 16 | 5.8 |
| | Aug. 22 | 24.3 | 108 | 7.0 |
| 18. Sand Ridge | Aug. 22 | 24.5 | 106 | 7.0 |

* Crab-Orchard Creek itself was too turbid to allow colorimetric work. Its effect upon the river indicates a high acidity. A heavy rain fell Aug. 20–21, which probably accounts for the decrease in alkalinity between this sample and the samples taken at the entrance of Beaucoup Creek.

worst conditions to which the locality is subjected. The most characteristic animals of this group were the fresh-water shrimp, *Palaemonetes,* and the Unionidae. Shrimp were found in abundance in almost every part of the stream, as well as in the Little Muddy and Beaucoup Creek, sometimes as many as ten being taken in one scoop of the dredge net. They were found not only during the summer trip, but also in February in the more strongly acid water. The idea that this delicate little animal, said to be highly susceptible to many forms of contamination, may be quite resistant to acid is further substantiated by observations made by the author during the summer of 1918 on Lake Depue, Illinois, where it was found in acid waters near the inlet of waste from a zinc and sulphuric acid plant.

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Of the Unionidae the following nine species were identified:

*Quadrula pustulosa* (Lea)
*Amblema undulata* (Barnes)
*Tritigonia tuberculata* (Barnes)
*Eurynia luteola* (Lamarck)
*Anadonta grandis* (Say)
*Proptera purpurata* (Lamarck)
*Megalonias heros* (Say)
*Lampsilis anadontoides* (Lea)
*Elliptio gibbosus* (Barnes)

The distribution of the various species appeared to be influenced by the character of the bottom rather than of the water, since the heavy-shelled forms were invariably found in the upper part of the stream where the bottom is coarse gravel, and the thin-shelled forms nearer the mouth where the bottom is clay and fine sand. A careful survey for about three fourths of a mile revealed no living mussels in the Little Muddy, although apparently recent shells of *Lampsilis anadontoides* were common. One very striking characteristic of the mussels of the Muddy River was the corrosion of their shells, due, no doubt, to the acidity of the water. Although clams were strikingly abundant, no perfect specimens were found, for, even in the very young ones, the umbonal markings had entirely disappeared, while older specimens were extensively corroded.

Abundant as were the mussels in the Big Muddy River, only two snails (individuals) were found; one a living *Pleurocera elevatum* taken opposite Benton (fig. 1), the other a *Campeloma subsolidum* taken near Murphysboro. No dead shells were found to indicate that snails had ever been present. This is in striking contrast to the other streams of Illinois, most of which are rich in gill-breathing snails. Equally conspicuous for their absence were the nymphs of the burrowing may fly, *Hexagenia*. In late summers this form literally honeycombs the muddy sides of pools in the Vermillion and Sangamon rivers. Not one was seen in the Muddy. Nymphs of the dragon flies were also lacking, although two larvae of *Corydalis cornuta* and any number of chironomid and mosquito larvae were taken.

Fish were everywhere abundant. Dog fish, sun fish, and native carp were taken with the hook and line, while large numbers of minnows, cat fingerlings (at one time a school of several hundred), and unidentified fry were seen in the shallow pools and riffles. There were also numerous swarms of top minnows, while gar, fifteen to eighteen inches in length, were seen in ever-increasing numbers toward the mouth of the river.

## Discussion

The study of an acid stream, such as the Big Muddy, is of twofold significance; first, in determining the relative susceptibility of different forms of animals at different stages of their development to hydrogen-ion concentrations, and, second, in assisting in the interpretation of experimental data. While no conclusions can be drawn from a single examination of one stream,

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it would be of great interest to know, for example, whether branchiate snails and may-fly nymphs are universally absent from acid waters.

The large number of fish fry and fingerlings observed in the upper waters of the stream furnish another problem of interest. These fish must have hatched and undergone the earliest most susceptible stages of their life histories during the period of spring rains while the stream was still receiving strongly acid mine waters. It is improbable that they could have migrated up from the Mississippi since then. At the same time it is possible that the waters of the river were less acid in April and May than when tested in February. In the absence of data on this point no conclusions can be drawn, but this is cited as one of the problems to be solved only after a continuous study of an acid stream with water analyses at frequent intervals throughout at least an entire year.

Six years ago M. M. Wells (5) concluded, from the behavior of fish in gradients of acid and basic waters, that the optimum reaction of water for fish is alkaline and near the turning point of phenolphthalein. (This would be about $P_H$ 8.) Since then others have gotten similar results. But Wells was working with fish from the Vermillion River, a basic stream, $P_H$ about 8. Had he been working with fish from the Big Muddy River, it is probable his findings would have been different. The results of Wells and of those who followed him are good, but they apply not to fish in general, but to fish from a particular alkaline stream. When fish from acid streams have also been studied, it may appear that fish can readily become acclimated to hydrogen-ion concentrations within a considerable range (say $P_H$ 6 to $P_H$ 8.5 at ordinary temperatures), but are exceedingly sensitive in avoiding a change from the hydrogen-ion concentration to which they are accustomed.

Again, it has been suggested that the sensitivity of fish to domestic sewage is a sensitivity to the increased acidity of the water due to the carbon dioxide liberated by organic decomposition. Samples of water from the bottom of the Illinois River between Depue and Henry, Illinois (foul-smelling water from which free oxygen had been entirely absorbed by decomposing sewage, and in which only bacteria and sludge worms could live), showed a $P_H$ value about 7.5, while water from the Big Muddy, in which were delicate young fish, had a $P_H$ value of 6.8. Are hydrogen-ion concentrations in this range a controlling factor in fish distribution? The author has shown in a previous paper (3) that at room temperatures variations in the hydrogen-ion concentration of water between about $P_H$ 6.7 and 7.5 have no detectable effects upon the rate or amount of regeneration in tadpoles, but that greater fluctuations in the direction of either acidity or basicity produce marked decreases in regeneration. A careful study of our acid streams might discover similar ranges of hydrogen-ion concentration to which the various species may become accustomed, but beyond which their continued existence in the stream becomes impossible.

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While this study of the Big Muddy River was interrupted before anything more than a hurried preliminary survey had been made, it does serve to emphasize the necessity of close cooperation between field and laboratory studies. At present our knowledge of the rôle in development and distribution of fresh-water animals played by the hydrogen-ion concentration of the water is based almost entirely upon laboratory studies, and stands in need of a careful detailed study at all seasons and all water levels of a few of our acid streams.

## Conclusions

1. The hydrogen-ion concentration of the water of the Big Muddy River was found to vary between $P_H$ 5.8 and $P_H$ 6.8 to 7.2, the higher acidity occurring during the winter.

2. The bottom fauna was characterized by the abundance of clams and shrimp, and by the absence of branchiate snails and ephemerid nymphs.

3. Fish fry and fingerlings were found in large numbers during the summer in weakly acid water, $P_H$ 6.8.

4. Observations on our acid streams, continued over a considerable period of time, would tell us much concerning the adaptability of various species to different hydrogen-ion concentrations and are greatly needed in the interpretation of experimental data.

## Acknowledgment

Funds for this investigation were furnished by the Illinois State Water Survey. The author is also indebted to Mr. F. C. Baker, Curator of the Museum of Natural History, University of Illinois, for identification of the Unionidae.

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# SOME FACTORS AFFECTING THE DISTRIBUTION OF THE PRAIRIE VOLE, FOREST DEER MOUSE, AND PRAIRIE DEER MOUSE[1]

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The study of the climatic factors limiting animal distribution has been carried on almost entirely by the statistical method, attempting to correlate the limits of distribution of the various species, genera, or larger groups with certain isotherms or similar lines of meteorological averages. Few experiments have been performed to determine whether or not the factors believed to be critical in distribution have an actual vital importance for the individuals of the species concerned. For no species of mammal have the limits of toleration for temperature, humidity, and other climatic factors been correlated with the degrees of temperature, percentages of humidity, and so forth, making up the immediate environment of the animals. Neither for any form has the water and food requirements of the individuals been determined in relation to the amounts of water and food present in nature. Critical studies of these factors must be made for many species before we shall know which factors are most important in the control of mammalian distribution.

In 1917 some preliminary experiments were begun at the Kansas State Agricultural College, Manhattan, Kansas, to determine the factors which limit the prairie deer mouse, *Peromyscus maniculatus bairdii* (Hoy and Kennicott), to the open fields, and the forest deer mouse, *Peromyscus leucopus noveboracensis* (Fischer), to the woods. These experiments indicated that the forest form used more water than the prairie form, and as there would possibly be less water available on the prairie than in the forest, this factor might limit the forest form to the wooded areas.

In the spring of 1919 an opportunity was had to test this factor thoroughly in the laboratory of Dr. V. E. Shelford. Thanks are due Dr. Shelford for the free use of the facilities of the laboratory and for much helpful advice.

While collecting the prairie deer mice to use in the experiments the prairie vole, *Microtus ochrogaster* (Wagner), was secured in abundance and this species was included in the series of experiments.

The three species studied are common throughout a large part of the upper Mississippi Valley. The habitats of the prairie deer mouse and of the

[1] Contribution from the Museum of Zoology, University of Michigan, and the Zoological Laboratory, University of Illinois.



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prairie vole are the open fields, though the prairie deer mouse is also found, but rarely, in open shrubs at the edges of fields. The forest deer mouse lives mostly in heavy forest, though it is sometimes found among shrubs or in orchards and rarely even in low shrubs along fences. The habitat limitations of these forms is very marked, and, though there is a slight amount of overlapping on the border between forest and prairie, the prairie species are not found in the forest nor the forest form on the prairies.

The aim of the experiments was to determine the quantity of water used by each of the species at different temperatures and at different air humidities. The amount of food eaten at the different conditions was also determined. In addition, a little data was obtained on the toleration of the various species at temperatures and humidities ranging from 0° C. to 39° C. and with humidities at certain of the temperatures from about 5 percent to 95 percent. No attempt was made to determine whether the food and water requirements at different seasons varies independently of the external conditions.

## Experimental Methods

The stock of animals for the experiments was secured by trapping in the fields and woods about Urbana, Illinois, during the spring of 1919. Box traps were used which did not injure the animals in any way, and a nest of cotton was provided in each trap, so that the animals would not suffer from the cold after they were caught.

The animals not actually being used in experiments were kept in open wire cages in a greenhouse connected with the laboratory and were fed the same food and given water in the same way as when in an experiment. Animals were kept singly at all times, and not more than one was ever allowed to occupy the same cage. In each cage was a nest of dried grass.

The conditions in the greenhouse fluctuated somewhat with the outside weather conditions, though the temperature in the greenhouse never rose higher than 35° C. and never fell below 13°. For most of the spring the range was from about 20° to 30°. The humidity averaged rather low. In general the temperature rose and the humidity fell during the day, and the temperature fell and the humidity rose during the night.

When being transferred from the cages to the experimental jars, or when being weighed, the animals were always handled in a small tin box with a sliding cover; they were handled and excited as little as possible. By placing the small weighing box over the nest cylinder and turning both upside down the mouse would usually drop into the box without any excitement. The mice were weighed to tenths of grams on a very delicate analytical balance at the beginning and end of every experiment and sometimes more frequently.

The jars in which the experiments were carried on were, with a very few exceptions, battery jars 6 inches in diameter and 8 inches in height. For a

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few experiments battery jars 6½ x 9 or 8 x 12 inches were used; and in the experiments at 15° and at temperatures of 37° to 39° a 5 x 7 battery jar was used.

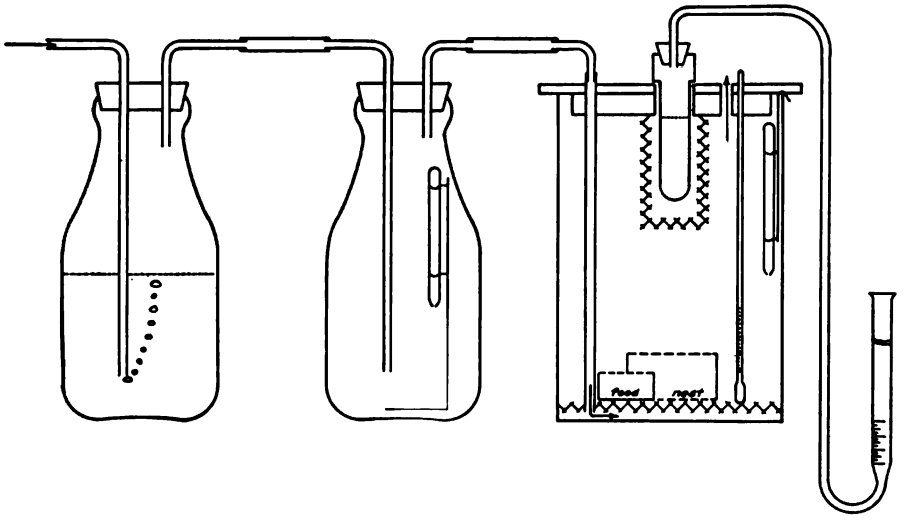


FIG. 1. Diagram of experimental jar and attachments. The first bottle in the air supply line (first on left) contains water or sulphuric acid; the second bottle contains a control water tube. In the experimental jar (on right) may be seen the cylindrical evaporimeter at the top, the thermometer, tube of drinking water, food box and nest.

Each jar was provided with its own air supply and operated as a unit, entirely independent of every other experiment. Never more than one individual animal was placed in a jar. Each jar was covered at the top by a wooden cover having holes for the entrance of the various instruments and tubes. At the bottom of the jar was a sheet of large-meshed screen, through which the feces or waste fell. The pan for the food was large enough so that the mouse could get entirely inside it for feeding; there was thus little tendency for food to be carried outside to be wasted, although any waste could be recovered from under the screen. The nest of dried grass was placed inside a short tin cylinder fully open on both top and bottom for the circulation of air.

Water was supplied by a test tube of which the mouth had been closed off in a flame until an opening about 2 mm. remained. When filled with water and inverted in the cage the mouse could lick the water from the bottom without any tendency to waste the water and without any danger of contamination with dirt. Each day, or less frequently, the amount of water used by the animal could be determined by filling the tube with a burette. The loss by evaporation from the tube was determined by control tubes of

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the same type inserted in large bottles in the air supply line. The evaporation from these control tubes, owing to a more rapid air flow, would be somewhat greater than in the experimental jars, but the total amount is so low, 0.0 to 0.25 c.c. daily, that the error is negligible. Distilled water was used exclusively.

A thermometer was hung in each jar with the bulb at the level the body of the mouse would occupy.

At the top of each cage was inserted a common cylindrical atmometer cup which projected through the cover so that all the evaporating surface was exposed inside the jar. Tests with instruments in both the normal upright position and inverted as here indicated that the evaporation was practically identical in either position, and also that the evaporation at the top of the jar, for the rate of air flow used, was the same as that at the bottom. Each atmometer was connected with a burette graduated in tenths of cubic centimeters, and was surrounded with a large-meshed screen to prevent the mice getting the surface of the cup dirty as they climbed about the jar. This screen did not interfere with the evaporation to any appreciable degree. The atmometer cups were standardized at the beginning of the series of experiments and also at the end, and the standard evaporation for each experiment computed.

The temperature of the experiments was determined by that of the room in which the jar was placed. Two rooms were available with temperatures maintained approximately at 21° C. and 28°, respectively, and controlled by automatic devices connected with heating coils and with refrigerating coils. In addition, a number of experiments were carried on in a cold cabinet having a temperature constantly around 0° C.; and a few experiments were carried on in a cabinet having a temperature of 15° C. The experiments with temperatures above 30° were performed in incubators of the ordinary laboratory type.

The rooms with constant temperatures of 21° and 28° were lighted by daylight from the north, and, in addition, were provided with daylight lamps of large size which burned from 6 A.M. to 6 P.M. The cold cabinets and incubators were not lighted, and all experiments in them were carried on in the dark.

In the 21° and 28° rooms thermographs on the same shelf as the experimental jars gave constant records of the temperature. The readings of these thermographs never varied more than a degree or two from the readings of the thermometers in the jars. In computing the average temperatures of the experiments run in these rooms the average temperature as computed from the thermograph records was combined with the average from the readings taken twice or more often each day from the thermometer in the jar itself, equal weight being given to each. During most of the experiments in these two rooms maxima and minima thermometers were maintained in jars on the

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same shelf with the experimental jars, and with air from the same source; when available, readings from these thermometers are used for stating the maxima and minima temperatures; when not available, the maxima and minima readings from the thermograph are used.

The air supply was taken from the University mains through a reducing valve, and the supply to each experimental jar was provided with a control valve. For each jar the air flow was regulated so that the amount per minute would equal the capacity of the jar. For the 6 x 8 jars this was about four liters. The air flow was frequently tested by the delicate gauges described by Hamilton[2] and the rate of flow maintained at a constant amount.

The dry air of the 21° and 28° rooms was made by mixing air dried by passing over freezing coils and air saturated by a water bath, the mixture of the two being controlled by humidostats. The percentage of humidity in the dry air of each of these rooms, however, varied considerably, a variation of 5 percent of humidity in the 21° room and 10 percent of humidity in the 28° room being common. These variations were rapid, the range from dryest to wettest limits often taking no more than ten minutes. To secure very dry air the air was bubbled through several jars of sulfuric acid, while for very moist air it was bubbled through bottles of water. The humidity in these conditions was very constant. The air in the zero cabinet was always saturated with moisture. The air used in the incubators was taken through a reducing valve directly from the University mains, no humidostat being used, and the amount of fluctuation in humidity was very small. The dry air in these incubators was bubbled through sulfuric acid and the moist air through water.

Each day, or several times a day, the humidity of each different kind of air being used was determined by a psychrometer inserted in the pipe line supplying air to the experimental jars. From the depression of the wet bulb thermometer the relative humidity was determined according to the psychrometric tables published by the United States Weather Bureau; and the vapor pressure deficit was determined from the Smithsonian Meteorologic tables, fourth edition, by subtracting the actual vapor pressure in each case, as calculated from the readings of the wet and dry bulb thermometers, from the vapor pressure of saturated air at the same temperature. No correction was made in these calculations for changes in barometric pressure, this being taken as constantly 30.0 inches.

## Water Requirements

A careful study of Table II shows that the prairie deer mouse does not use less water per day than does the forest form. The considerable series of experiments at 21° in dry air shows almost exactly the same average water consumption per individual in the two species (1.74 and 1.72 c.c.). At 28°

[2] Hamilton, Clyde C., Biol. Bull. 32: 161–164, 1917.

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TABLE I. *Meteorological data. Experiments with dry food*

| Total days in experiments | Temperature | | | | | Relative humidity | | | | | Vapor pressure deficit | | | | | Evaporation standard. Averages per day | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Averages | | | Extremes | | Averages | | | Extremes | | Averages | | | Extremes | | | | | |
| | All | Low | High | Min. | Max. | All | Low | High | Min. | Max. | All | Low | High | Max. | Min. | All | High | Low | |
| | ° C. | ° C. | ° C. | ° C. | ° C. | % | % | % | % | % | mm. | mm. | mm. | mm. | mm. | c.c. | c.c. | c.c. | |
| 27 | .04 | −0.1 | 1.3 | −2.0 | 3.0 | 100 | 100 | 100 | 100 | 100 | .000 | .000 | .000 | .000 | .000 | ..... | ..... | ..... | 0°, wet air. |
| 217 | 20.5 | 19.8 | 21.2 | 15.0 | 28.9 | 47 | 37 | 57 | 25 | 68 | 3.633 | 4.836 | 2.718 | 5.182 | 1.727 | 5.56 | 6.83 | 3.40 | 21°, dry. |
| 19 | 20.5 | 20.4 | 20.9 | 16.0 | 21.7 | 93 | 92 | 94 | 86 | 95 | 0.440 | 0.534 | 0.356 | 0.864 | 0.279 | 1.26 | 1.54 | 0.96 | 21°, wet. |
| 32 | 27.9 | 27.5 | 28.2 | 25.0 | 32.2 | 6 | 5 | 9 | 1 | 18 | 8.721 | 9.144 | 8.433 | 9.855 | 7.214 | 16.54 | 17.72 | 15.64 | 28°, very dry. |
| 87 | 27.8 | 27.4 | 28.4 | 22.0 | 32.2 | 35 | 18 | 40 | 12 | 61 | 5.243 | 5.690 | 4.928 | 8.103 | 2.819 | 10.05 | 12.25 | 8.48 | 28°, mod. dry. |
| 20 | 28.0 | 27.4 | 28.3 | 22.2 | 32.2 | 92 | 91 | 95 | 88 | 96 | 0.589 | 0.711 | 0.356 | 1.168 | 0.279 | 1.38 | 1.73 | 1.26 | 28°, wet. |
| 28 | 32.6 | 31.7 | 33.9 | 31.4 | 35.0 | 27 | 18 | 33 | 16 | 34 | 6.811 | 8.001 | 6.121 | 8.407 | 6.071 | 18.02 | 21.74 | 14.98 | 32–34°, dry. |
| 22 | 32.9 | 31.5 | 34.3 | 30.6 | 34.1 | 90 | 84 | 94 | 84 | 100 | 0.757 | 1.295 | 0.443 | 2.438 | 0.000 | 2.79 | 3.69 | 2.28 | 32–34°, wet. |
| 7 | 36.1 | 35.8 | 36.3 | 35.8 | 36.4 | 28 | 28 | 29 | 26 | 30 | 7.199 | 7.264 | 7.122 | 7.569 | 6.960 | ..... | ..... | ..... | 35–36°, dry. |
| 11 | 35.2 | 34.5 | 36.3 | 34.0 | 36.7 | 68 | 55 | 85 | 51 | 87 | 2.803 | 3.810 | 1.989 | 4.191 | 1.016 | 2.48* | ..... | ..... | 35–36°, wet. |
| 9 | 37.2 | 37.1 | 37.8 | 37.0 | 38.2 | 26 | 23 | 32 | 21 | 32 | 7.702 | 8.153 | 7.137 | 8.459 | 6.985 | 18.89 | 20.08 | 17.80 | 37–38°, dry. |
| 4 | 37.6 | 37.0 | 37.8 | 37.0 | 38.5 | 77 | 73 | 79 | 70 | 83 | 1.879 | 2.337 | 1.727 | 2.032 | 1.422 | 8.71 | 12.10 | 5.32 | 37–38°, wet. |
| 2 | 39.1 | 39.0 | 39.2 | 38.9 | 39.4 | 34 | 32 | 35 | 32 | 38 | 6.858 | 7.163 | 6.553 | 7.315 | 6.121 | ..... | ..... | ..... | 39°, dry. |

* Record for only one experiment.

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the prairie form in these experiments used slightly more water than the forest form, though at 32–34° the forest mouse used a slightly greater amount than the prairie mouse. The differences at any of the conditions are not great enough to be beyond the limits of individual variation.

TABLE II. *Water drunk per day per individual*

| *Microtus ochrogaster* | | | | *Peromyscus m. bairdii* | | | | *P. l. noveboracensis* | | | | Environmental conditions |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total days | Average c.c. | From c.c. | To c.c. | Total days | Average c.c. | From c.c. | To c.c. | Total days | Average c.c. | From c.c. | To c.c. | |
| 20 | 6.40 | 5.93 | 6.88 | 20 | 1.98 | 1.24 | 2.72 | 29 | 1.54 | 1.36 | 2.29 | 21°, dry air; males. |
| 51 | 5.81 | 3.99 | 9.64 | 59 | 1.66 | 1.12 | 2.39 | 29 | 1.91 | 1.44 | 2.15 | 21°, dry; females. |
| 71 | 5.98 | 3.99 | 9.64 | 79 | 1.74 | 1.12 | 2.72 | 58 | 1.72 | 1.36 | 2.29 | 21°, dry; all adults. |
| .... | ..... | .... | .... | 5 | 3.78 | .... | .... | 5 | 6.22 | .... | .... | 21°, dry; before parturition. |
| 11 | 14.23 | .... | .... | 16 | 2.98 | .... | .... | 16 | 6.36 | .... | .... | 21°, dry; nursing. |
| 11 | 5.87 | 4.43 | 7.60 | 10 | 1.92 | 1.68 | 2.16 | 11 | 1.74 | 1.38 | 2.05 | 28°, very dry. |
| 31 | 4.33 | 3.31 | 5.26 | 35 | 2.12 | 1.81 | 2.50 | 21 | 1.64 | 1.48 | 1.79 | 28°, moderately dry. |
| 9 | 4.00 | 3.75 | 4.25 | 11 | 2.31 | 1.55 | 3.37 | 8 | 2.49 | 2.06 | 2.74 | 32–34°, dry. |
| 12 | 6.46 | 3.20 | 9.25 | 7 | 1.14 | 1.07 | 1.23 | 3 | 2.16 | .... | .... | 32–34°, wet. |
| 4 | 2.95 | .... | .... | 1 | 1.90 | .... | .... | 4 | 3.77 | .... | .... | 35–36°, dry. |
| .... | ..... | .... | .... | 5 | 1.50 | 1.40 | 1.65 | 6 | 1.35 | 1.05 | 1.95 | 35–36°, wet. |
| .... | ..... | .... | .... | .... | .... | .... | .... | 2 | 4.10 | .... | .... | 37–38°, dry. |
| .... | ..... | .... | .... | 3 | 2.33 | 1.80 | 3.50 | .... | .... | .... | .... | 37–38°, wet. |

These mice would, of course, obtain some water from the food which they ate, but as the individuals of both species ate about the same quantity of the same kinds of food the relative amount of water obtained is not appreciably changed.

Females just before parturition and mothers nursing young use much more water than females at other times. This seems to be true of all the three species studied, although no records are at hand for the prairie vole immediately preceding parturition, and only one record for the prairie deer mouse and one for the forest deer mouse. In these experiments the forest form, just preceding parturition and while nursing young, used more water than the prairie form. However, the forest mother was nursing four young while the prairie mother was nursing only two, which may account for part of the difference in water consumption. Also, when more records are available the differences in water consumption of these two females may prove to be partly due to individual variations. Even if pregnant females and nursing mothers of the forest form should prove to require more water than females of the prairie form in the same conditions this factor will not explain the habitat limitations of the males nor of the other females in the two species.

At 21° in dry air there seems no difference between males and females in water consumption, except as this is influenced by differences in individual weight. From Table II it is seen that the males of the prairie vole and of the prairie deer mouse used on the average slightly more water than the

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females, while in the forest deer mouse the reverse is the case. However, the males of the prairie vole and of the prairie deer mouse in this set of experiments averaged heavier than the females, while the males of the forest deer mice were lighter on the average than the females. The averages of the water consumed per gram body weight show little difference between males and females of either species, and in each species the limits of variation in this ratio for one sex includes the maxima and minima of the other sex.

TABLE III. *Total water per gram body weight used by adults daily, water drunk plus water in food*

| *Microtus ochrogaster* | | | | *Peromyscus m. bairdii* | | | | *P. l. noveboracensis* | | | | Environmental conditions |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total days | Average c.c. | From c.c. | To c.c. | Total days | Average c.c. | From c.c. | To c.c. | Total days | Average c.c. | From c.c. | To c.c. | |
| 71 | .211 | .152 | .255 | 79 | .126 | .082 | .177 | 58 | .090 | .057 | .117 | 21°, dry air. |
| 11 | .190 | .125 | .292 | 10 | .126 | .119 | .133 | 11 | .082 | .075 | .087 | 28°, very dry. |
| 31 | .158 | .096 | .210 | 35 | .146 | .132 | .168 | 21 | .082 | .078 | .085 | 28°, dry. |
| 9 | .132 | .130 | .132 | 11 | .192 | .123 | .287 | 8 | .114 | .085 | .131 | 32–34°, dry. |
| 2 | .107 | .... | .... | 1 | .166 | .... | .... | 4 | .171 | .... | .... | 35–36°, dry. |
| .... | .... | .... | .... | .... | .... | .... | .... | 2 | .217 | .... | .... | 37–38°, dry. |

The forest mouse is much heavier than the prairie mouse, and if we consider the amount of water used per gram body weight (Table III), it will be seen that the prairie mouse uses much more water in proportion to its size than does the forest mouse.

It is fully evident from the results of these experiments that different water requirements can not be the factor causing the different habitat limitations of these two species of *Peromyscus*. The forest deer mouse can certainly live on just as little water as the prairie form under temperatures from 21° to 34° and with relative humidities as low as 7 percent.

In nature both of the deer mice probably secure most of their needed water from their food, most of which is not so dry as that provided in these experiments.

The prairie voles use much more water per individual than either species of the deer mice. If we consider the larger size of the voles, the difference is not so great; yet at 21° in dry air the prairie voles on the average use over 50 percent more water per gram body weight than the prairie deer mice and over twice as much as the forest deer mice. (See Table III.) In nature the prairie vole probably never lives entirely on dry food, but secures most or all of its water supply from the green grasses which form a great share of its food.

To determine if the quantity of water used by the different species was actually needed, an individual of each species was tested with an amount of water less than the average. One individual of the forest deer mouse and

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one individual of the prairie deer mouse were each given 1.00 c.c. of water daily for five days, and one individual of the prairie vole was given 2.00 c.c. of water daily for the same length of time. These experiments were all at 21° in dry air, and are directly comparable with the series of experiments under these conditions in which an ample supply of water was constantly present. All the animals were fed an abundance of dry food; wheat and peanuts for the deer mice, and rolled oats and dried grass for the vole.

The prairie vole receiving the reduced amount of water lost 6.2 grams in weight in the five days; the prairie deer mouse lost 1.4 grams; and the forest deer mouse lost 2.7 grams. In the series of experiments (Table VI) under these same conditions, only with an abundance of water, all the prairie voles and all the forest deer mice gained in weight, and none of the prairie deer mice lost more than 0.9 gram in ten days, a period twice as long as the present experiment.

The mice receiving less than the normal amount of water, after the first day, often gave evidence of thirst. They were more active than normal, and they often tried to bite the end of the dry water bottle or other parts of the cage. When given their daily allotment of water they usually drank a considerable part of it at once. This behavior was much the same in all three species.

The conclusion seems justified that the mice in all the experiments where an abundance of water was present were drinking little if any more than they actually needed to sustain health.

There seems no positive difference in the amount of water consumed by either of the species at 28° and at 21°. At other temperatures there is not a sufficient number of experiments for comparison, as there is much individual variation in the amount of water consumed. Some individuals seem to show a decidedly increased water consumption at temperatures above 30°, but the number and length of the experiments are too scanty to be conclusive. At temperatures of 21° and 28° all the species used less water in the wet air than in the dry air, owing to the food absorbing moisture.

At 28° the forest deer mice used on the average slightly more water in very dry air than in the moderately dry air, but one individual used more water in the moderately dry air than in the very dry air. The prairie deer mice use on the average more water in the moderately dry air than in the very dry air, though one individual used almost exactly the same amount in both conditions (2.15 and 2.16 c.c., respectively). There is considerable variation in the amount of water used by these mice, and it is apparent that with these species at this constant temperature there is no very definite difference in the water consumption between relative humidities averaging about 7 percent and those averaging about 35 percent.

The prairie vole, on the contrary, seems to show a more definite relation of water use to humidity, two individuals using a greater amount of water

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in very dry than in moderately dry air. It is possible that with a larger series of experiments this difference might prove to be due to coincidence.

## Food Requirements

Food is probably not a factor limiting the habitat distribution of the two species of *Peromyscus* considered. Both, so far as is known, live on the same kind of food—grains, seeds, insects, fruits, etc. In captivity both thrive on the same diet of wheat and peanuts. They are also fond of rolled oats. In eating grains of wheat the outer coat, the bran, is removed. In removing the bran the forest mouse is rather wasteful, often removing a considerable amount of the heart of the grain along with the bran, but the prairie form is very economical, seldom discarding more than the thin outer coat of the grain. These habits may be correlated with a greater scarcity of food in the prairie habitat, but economy or wastefulness of food can hardly be a factor limiting either species in its habitat distribution.

Both of these mice eat flesh when it can be obtained. One female of the prairie deer mouse in these experiments partly ate at least two of her own young. A nestful of young were born April 19 in an experimental jar at 21° in dry air. They were not disturbed or counted at that time, but four days later two of the young were discovered partly eaten by the mother, and there seemed no doubt that they had been killed by her. During this time she was being fed wheat alone. I then began to feed her in addition a roasted peanut kernel daily and the two remaining young grew safely until they were sixteen days old, when the experiment was closed. Another mother of this species in an experiment at 28° in dry air safely raised all her young, as did one of the forest deer mice in an experiment at 21° in dry air. Both of the latter were fed peanuts as well as wheat.

The food used in all the experiments, with one exception, on the two forms of deer mice was dry whole grains of wheat and peanut kernels with the hulls and brown covering removed. They were given all the wheat they would eat, and on the average about one small peanut kernel (0.5 to 0.7 gram) per day. A young prairie deer mouse in an experiment in dry air at 21° refused to eat the peanuts and did not eat the whole wheat well, and was therefore given rolled oats instead.

The prairie deer mice in the experiments at 21° in dry air ate on the average 1.86 (1.35 to 2.93) grams of whole wheat grains per day at the same time that they were using an average of .48 gram of peanut kernels per day. A female under these conditions just before parturition and while nursing two young ate considerably more than the average amount of food, using 3.12 grams of wheat and .50 gram of peanuts per day. At 28° in dry air the average food used by normal adults was 1.45 (0.80 to 2.09) grams of wheat and .43 gram of peanuts.

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The forest deer mouse at 21° in dry air used on the average 2.73 (1.99 to 3.23) grams of wheat and .61 gram of peanuts daily. A female just before parturition and while nursing four young ate 2.90 grams of wheat and .70 gram of peanuts per day. At 28° in dry air 2.07 (1.31 to 2.84) grams of wheat and .71 gram of peanuts daily were eaten on the average by normal adults.

TABLE IV. *Calories in food eaten per day per gram body weight*

| *Microtus ochrogaster* | | | | *Peromyscus m. bairdii* | | | | *P. l. noveboracensis* | | | | Environmental conditions |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total days | Average | From | To | Total days | Average | From | To | Total days | Average | From | To | |
| 4 | .538 | .... | .... | 9 | .816 | .610 | 1.047 | 6 | .633 | .... | .... | 0°, wet air. |
| 71 | .514 | .424 | .622 | 79 | .552 | .480 | .699 | 58 | .518 | .341 | .642 | 21°, dry, all adults. |
| 20 | .561 | .530 | .592 | 20 | .536 | .511 | .560 | 29 | .554 | .423 | .642 | 21°, dry, males. |
| 51 | .476 | .424 | .622 | 59 | .558 | .480 | .699 | 29 | .481 | .341 | .561 | 21°, dry, females. |
| .... | .... | .... | .... | 10 | 1.205 | .... | ..... | 9 | .355 | .... | .... | 21°, dry, juv. |
| .... | .... | .... | .... | 9 | .576 | .535 | .627 | 10 | .364 | .272 | .455 | 21°, wet. |
| 11 | .305 | .274 | .343 | 10 | .434 | .418 | .449 | 11 | .399 | .373 | .431 | 28°, very dry. |
| 31 | .391 | .292 | .524 | 35 | .451 | .360 | .528 | 21 | .460 | .381 | .532 | 28°, dry. |
| .... | .... | .... | .... | 10 | .563 | .518 | .593 | 10 | .381 | .325 | .437 | 28°, wet. |
| 9 | .195 | .160 | .223 | 11 | .348 | .208 | .615 | 8 | .329 | .267 | .366 | 32–34°, dry. |
| 12 | .284 | .214 | .509 | 7 | .459 | .427 | .502 | 3 | .423 | .... | .... | 32–34°, wet. |
| 2 | .166 | .... | .... | 1 | .339 | .... | ..... | 4 | .261 | .... | .... | 35–36°, dry. |
| .... | .... | .... | .... | 5 | .326 | .294 | .347 | 6 | .404 | .312 | .590 | 35–36°, wet. |

The forest mouse evidently eats more food than the prairie form; but this seems to be due to its larger size, for the number of calories used per day per gram of body weight is nearly the same in the two species (Table IV), being slightly larger for the smaller species.

The principal natural food of the prairie vole is green grass. In captivity they also readily eat dried grasses if supplied with water. They seem fond of dandelion leaves and stems, and in nature would probably eat these and other herbs. Raw potatoes are much liked by them, and they undoubtedly eat roots, bulbs, and tubers when these are available. They readily eat rolled oats, but if other food is available they refuse hard seeds such as whole grains of wheat and dry corn; however, they would probably eat grain and weed seeds soaked up by lying on wet ground.

In the experiments on dry feed the voles were fed rolled oats and dried grass. The dried grass was mostly blue-grass gathered in the yard of the laboratory and allowed to dry in the greenhouse. The animals did not do well on rolled oats alone. On this rich food they all became very fat.

At 21° in dry air the average amount of food consumed by the voles was 3.31 (2.08 to 4.80) grams of rolled oats and .94 gram of dried grass per day. At 28° in dry air the averages were 2.35 (1.94 to 2.68) grams of rolled oats and .83 gram of dried grass.

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The prairie vole uses slightly less calories per gram of body weight than the deer mice. This would be expected on account of its larger size.

In general the animals in these experiments which used the most food were those which were gaining weight the most rapidly, but this was by no means always the case. Some means of expressing the amount of food used in proportion to the gain or loss in weight would be desirable, but the number of experiments at any one temperature are too few in number to justify the attempt here.

The water content and food value of the different foods used have been taken to be the following:

| | | | | | | |
|---|---|---|---|---|---|---|
| Whole wheat grains..... | 10.6% | water | 3.33 | calories | per | gram |
| Peanuts, edible portion..... | 9.2% | " | 5.48 | " | " | " |
| Rolled oats..... | 7.7% | " | 3.97 | " | " | " |
| Dried blue-grass..... | 7.7% | " | 1.98 | " | " | " |

Less food is used by all the species at the higher than at the lower temperatures. This is evidently due to the smaller loss of body heat by radiation and conduction at the higher temperatures.

It is impossible with the data obtained to determine any certain difference in the amount of food consumed under different humidities at the same temperatures.

No effect of sex on the amount of food used could be found, except that nursing mothers and females carrying young use much more food than other females. The number of experiments on young individuals is too few to use as the basis for any conclusions in regard to the amount of food used at different ages.

Nine experiments with an average length each of twelve days are available to show the effect of a constant diet of green grass alone on the weight of the prairie vole under greenhouse conditions. The temperatures and humidities in the greenhouse were constantly fluctuating, but the average temperature was 21.8° and the average standard evaporation was 15.2 c.c. per day. The mice were given a plentiful supply once daily, or sometimes more often, of green grass freshly cut in the laboratory yard, mostly blue-grass. No other food or water was supplied. Under these conditions the voles gained on the average 0.19 gram per day in weight, the greatest loss in weight being 0.41 gram and the greatest gain 0.74 gram per day. Only three of the nine voles lost in weight and only one lost at the rate of more than 0.06 gram per day.

A number of experiments were performed to test the ability of adults of the prairie vole to live on green food alone at constant temperatures. The results are presented in Table V. The voles in these experiments were fed green grass alone, with no water or other food. The entering air was either wet or dry as in the other sets of experiments under controlled conditions,

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but owing to the rapid evaporation from the green grass the humidity in the jars was raised above that of the entering air. For that reason the relative humidities in the jars are not those stated in Table I.

TABLE V. *Prairie voles fed green grass only, constant temperatures*

| Total days | Temperature, average | Evaporation, standard | Weights | | | | Environmental conditions |
|---|---|---|---|---|---|---|---|
| | | | Average beginning | Change per day | | | |
| | | | | Average | From | To | |
| | ° C. | c.c. | gms. | gms. | gms. | gms. | |
| 20 | 20.3 | 2.46 | 31.4 | .04 | −.31 | .65 | 21°, medium air. |
| 19 | 21.1 | 0.60 | 31.4 | .15 | −.01 | .32 | 21°, wet air. |
| 9 | 27.9 | 6.51 | 33.9 | .20 | −.01 | .38 | 28°, medium air. |
| 13 | 27.4 | 1.12 | 35.3 | .10 | −.14 | .38 | 28°, wet air. |

In these experiments the prairie vole shows his ability to live for periods at least as long as eighteen days and to gain weight on green grass alone under a variety of climatic conditions. The loss in weight by a few individuals must be due to other causes than a failure of the food to be sufficient for nutriment. This species in its native fields eats much grass and cut pieces of stems and blades are frequently found in its runways. Green grass evidently can supply the entire food and water of the species.

## TOLERATION OF EXTREME TEMPERATURES AND HUMIDITIES

For the determination of whether or not an animal can live and thrive under any given conditions of the environment the change of weight of the individual subjected to those conditions seems the most easily applied criterion. If the animal gains in weight it would seem to indicate that the conditions are favorable, while if there is a decided loss in weight it would seem to indicate an unfavorable environment. However, the animals do not always lose weight suddenly in an unfavorable environment, and prairie voles killed by high temperatures in some cases showed little loss in weight after death.

In using the criterion of change in weight as an indication of the favorable or unfavorable conditions of the environment it must be borne in mind that the animals are subject to considerable daily variations in weight. The amount of water drunk per day varies from about 1.0 c.c. to over 15.0 c.c.; and from nearly 2.0 to over 5.0 grams of food are eaten per day. Undoubtedly no animal eats and drinks all of its food or water at one time, but a variation of 1.0 gram in weight can not be of very great significance with these animals. With many or long-continued experiments the error due to time of weighing would tend to become minimized, especially as all the weigh-

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TABLE VI. *Average daily change in weight per individual, adults on dry feed*

| *Microtus ochrogaster* | | | | | *Peromyscus m. bairdii* | | | | | *P. l. noveboracensis* | | | | | Environmental conditions |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total days | Average beginning wt. | Change per day | | | Total days | Average beginning wt. | Change per day | | | Total days | Average beginning wt. | Change per day | | | |
| | | Average | From | To | | | Average | From | To | | | Average | From | To | |
| | gms. | gms. | gms. | gms. | | gms. | gms. | gms. | gms. | | gms. | gms. | gms. | gms. | |
| 9 | 31.8 | −.29 | −.62 | −.02 | 9 | 14.6 | −.22 | −.42 | .02 | 9 | 23.4 | −.17 | −.43 | −.03 | 0°, wet air. |
| 71 | 29.9 | .39 | .13 | .74 | 79 | 15.8 | −.02 | −.07 | .14 | 58 | 24.7 | .22 | .02 | .53 | 21°, dry. |
| ..... | ..... | ..... | ..... | ..... | 9 | 12.9 | .00 | −.05 | .04 | 10 | 27.8 | −.21 | −.34 | −.08 | 21°, wet. |
| 11 | 32.1 | .05 | −.05 | .18 | 10 | 16.6 | .01 | .00 | .02 | 11 | 24.3 | .21 | −.04 | .41 | 28°, very dry. |
| 31 | 29.0 | .27 | .06 | .71 | 35 | 15.9 | .01 | −.01 | .04 | 21 | 23.4 | .23 | .06 | .39 | 28°, mod. dry. |
| ..... | ..... | ..... | ..... | ..... | 10 | 15.2 | −.04 | −.10 | .05 | 5 | 29.1 | .14 | ..... | ..... | 28°, wet. |
| 9 | 31.6 | −.34 | −.45 | −.26 | 11 | 12.6 | −.09 | −.30 | −.05 | 8 | 24.4 | .04 | −.03 | .08 | 32–34°, dry. |
| 12 | 27.8 | .73 | .10 | 2.20 | 7 | 12.4 | .03 | −.03 | .07 | 3 | 25.8 | .26 | ..... | ..... | 32–34°, wet. |
| 4 | 28.6 | −.95 | ..... | ..... | 1 | 12.0 | −.40 | ..... | ..... | 4 | 22.9 | −.10 | ..... | ..... | 35–36°, dry. |
| ..... | ..... | ..... | ..... | ..... | 5 | 12.3 | .04 | .03 | .05 | 4 | 26.6 | −.05 | ..... | ..... | 35–36°, wet. |

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ing was done in the daytime when the animals are relatively inactive. But with a small number of short experiments, such as were performed at some of the extreme conditions, little dependence can be placed on small variations in weight. Even in those cases, however, a large variation would be significant. In the experiments at 21° and 28°, most of which were for 10-day periods, any average daily variation of less than 0.1 gram is not considered important.

All three species are able to live at a temperature of 0° C. with saturated air. One individual of the prairie vole (Table VI) lost weight heavily under these conditions, due evidently to a shortage in the amount of water supplied. Another individual, not given in the table, used more food than was anticipated and died after all the food supplied had been eaten. One individual of the prairie deer mouse also used all of its food the last day and was found to have lost 2.1 grams. In one experiment with a forest deer mouse the temperature in the experiment rose on the last day, due to an accident to the apparatus, and the frost melting from the brine pipes flooded the experimental jar. This unfavorable condition was undoubtedly partly the cause of the loss in weight by the mouse. In the other experiments under these conditions, in all three species, there was no decided loss in weight, and one of the prairie deer mice gained slightly.

Temperatures of 21° and 28° with either dry or wet air seem favorable for adults of all these species. At 21° with wet air a very fat forest deer mouse lost 1.7 grams in 5 days, but at these temperatures none of the other individuals showed a significant loss of weight. Young mice and voles also seem to do well under these conditions. One litter each of the prairie deer mouse and of the forest deer mouse were born at 21° in dry air under controlled conditions, and one litter of the prairie vole was placed in this environment when one day old; all grew and thrived, except that the four young of the forest deer mouse were quite thin at the end of 16 days, perhaps from some deficiency in the diet of the mother. A litter of the prairie deer mouse was born in an experiment at 28° with moderately dry air, and a litter of young of the prairie vole were placed in this environment at the age of two days. Both families grew and thrived.

The experiments above 28° were few in number and short in duration and can not be regarded to be conclusive as to the ability of the different species to withstand the various temperatures and humidities employed. The results obtained are here presented only as indicative of the limits of toleration in the species concerned.

At 32° and at 34° in dry air the prairie vole lost weight definitely, while the two species of *Peromyscus* show no definite gain or loss.

At 32° and 34° in wet air the prairie vole shows a decided gain in weight; while the two *Peromyscus* again do not show any definite gain or loss in the few experiments at hand.

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In dry air at a temperature averaging 35.8° (35.5 to 36.5) one prairie vole lost 1.9 grams in weight in two days. At temperatures around 36° with dry air one individual each of the prairie deer mouse and of the forest deer mouse lost weight slightly.

In air of a humidity of about 60 percent a prairie vole lived one day at a temperature ranging from 34.5° to 35.8°; the following morning the temperature had risen to 36.5° and the mouse was found dead. Another individual died in less than six hours at a temperature of 37.5° with the relative humidity at 70 percent. At a temperature of 37.0° to 37.1° and a relative humidity of 23 percent a third vole died in less than eighteen hours. Apparently a temperature around 36° in either wet or dry air is rather critical for this species, and an increase of temperature much above that point is fatal.

A female of the prairie deer mouse lived for five days at a temperature of 36.4° to 37.6° in air of 25 percent humidity with a loss of weight of only 0.8 gram. A male lost 1.5 grams in one day at 37.0° with 75 percent humidity, but a female lived two days at 37.1° to 38.5° and a humidity of 76 percent to 83 percent with a loss in weight of only 0.4 gram. A young female died in less than fifteen hours at 37.5° to 38.2° with 32 percent humidity. At 39.0° to 39.4° and a humidity of 35 percent an adult male died in less than a day.

A young female of the forest deer mouse lost 1.0 gram in two days at a temperature of 37.0° to 38.0° and a humidity of 30 percent. At 37.8° and a humidity of 78 percent an adult male died in less than twenty-one hours. At 38.9° to 39.1° and a humidity of 32 percent an adult female died in less than seventeen hours.

These experiments show that the two species of deer mice are very resistant to high temperatures, enduring temperatures which would be quickly fatal to the prairie vole. However, the data on toleration of high temperatures are too scanty to justify any conclusions as to the exact limits of toleration in the deer mice; neither does the data indicate any difference in the toleration of high temperatures between the two species.

## Discussion of the Results of the Experiments on Peromyscus

These experiments seem to prove conclusively that the amount of available water, either in the food or in a free state, can not be the factor limiting either the prairie deer mouse or the forest deer mouse to their respective habitats. Individuals of the two forms use almost exactly the same quantity of water. Neither can food be a factor of great importance in the habitat limitations of the species, for both seem to use the same kind of food.

While the number of experiments with extreme temperatures and humidities are few in number, they seem to indicate no important difference in the ability of the two forms to live at extremely high temperatures or in extreme conditions of humidity.

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These conclusions do not coincide with the results of a few experiments by Chenoweth,[8] who decided that high temperature, low humidity, or rapid air movement were fatal to the forest deer mouse. My experiments above described show that the forest mouse is able to live at a temperature of 28° for at least five days and not lose weight appreciably with a relative humidity of 5 percent. Also, forest deer mice in my experiments lived and thrived for four days at temperatures above 36°; none died except with temperatures over 37.5°. This species seems no less resistant to low humidities and high temperatures than the prairie deer mouse. I performed no experiments on the effect of rapid air movement.

Chenoweth does not describe his experiments well, but apparently he put the mice in bottles without food or water. It is probable that they died mainly from the lack of these essentials, though in his experiment with a high rate of air movement the rapid loss of body heat in the current of air might have been a contributing cause of death.

In my experiments at high temperatures the mice of all three species sometimes showed evident discomfort due to the heat. At these high temperatures they would seldom go into the nests, but could usually be found lying on the bottoms of the jars, breathing rapidly. At 28° no peculiar behavior whatever was noted in the experiments with low humidities. In none of my experiments, except those where the water supply was reduced, did I note any of the abnormal behavior described by Chenoweth.

In order to determine if there was any strong antagonism between the two species of *Peromyscus,* which might account for their habitat limitation, two adult males, one of each species, were placed together in a 6 x 8 battery jar and their behavior observed. These specimens had been kept since the time of their capture in individual cages, no two individuals even of the same species ever being placed together. When first placed together these two mice showed a slight antagonism, the prairie mouse attempting in a feeble way to ward off the approach of the forest animal. In less than a half minute, however, the antagonism completely vanished, and the two mice curled up together on the floor of the jar, where they remained for several hours. Evidently antagonism between these two species can not be an important factor in preventing one from invading the other's habitat.

These experiments then show no differences between the requirements for water, food, temperature, or humidity in the two species of *Peromyscus* sufficient to be the basis of their habitat differences. The requirements for water and food are nearly the same in the two forms and both can live and thrive over a wide range of the same temperatures and humidities. Evidently the limitation of the two species to different habitats must be due to differences in the behavior reactions by which they select their place of abode; and it is not due to the physical inability of either species to live in the habitat of the other.

[8] Chenoweth, Homer E., Biol. Bull. 32: 196–197, 1917.

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## Some Factors in the Distribution of the Prairie Vole

Fresh grass and other herbs are apparently the principal food of the prairie vole, and from this food the animals obtain also the water necessary for their existence. It has been shown by the previously described experiments that prairie voles can live and thrive on green grass alone without any additional water.

With dry food a supply of water is necessary, the amount needed averaging about 6 c.c. daily for adult voles at a constant temperature around 21° and with an air humidity of about 50 percent. The amount of water needed is not greatly different for other temperatures, up to 34°, or for other humidities, except that nursing mothers use much more water than other individuals.

As the habitat of the species is the upland prairies, where, during a dry period, no water other than that contained in the food would be available, it is evident that the species must be limited in its geographic distribution to regions furnishing a supply of green grass or herbage, roots, or tubers throughout the year. Periods of drought are of normal occurrence in the western part of the range of the species, and these droughts may occur in the winter months or at other times of the year as well as in summer. In middle Kansas, where part of the prairies dry up at times, the species is mostly limited in distribution to the heads of small coves where the vegetation stays green longer than on the hilltops. Farther west, where the whole of the prairies may dry up at times, the species is absent, and it seems probable that the occasional lack of available water or succulent vegetation is the factor limiting its westward distribution. Any water scarcity would fall most heavily on the nursing mothers, which require about twice the normal amount.

It may very well be that the southern limit of distribution for the prairie vole is determined by the maximum summer temperatures. The above-described experiments indicate that temperatures above 36° are critical for this species. These voles burrow, but they come out on the surface to feed. The ground in the fields where they live becomes very hot during the day, and the air temperature remains high during many nights in summer. Near the southern limit of the range of the species in Oklahoma and southern Missouri and farther south there must be numerous days in which the habitat is heated dangerously near the limit of 36° C. (96.8° F.).

The experiments throw little light on the temperatures which might determine the northern limit of distribution of the species. In the northern part of its range, southern Wisconsin and Michigan, the species undoubtedly endures temperatures much lower than the lowest experimented with (0° C.).

The experiments show that the species will thrive equally well in dry or wet air at 21°, and in very dry, moderately dry, or wet air at temperatures of 28°. At temperatures of 32° and above the few brief experiments performed indicate that the high humidity is more favorable than the low. At

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28° the animals seem to drink more water in very dry air than in moderately dry air (averages of 5.87 vs. 4.33 c.c. daily), though only two experiments of five days each were carried on in the very dry air.

At high temperatures, then, it is possible that low atmospheric humidity may have a deleterious effect, and this factor might under some conditions assist in limiting the westward distribution of the species. Very low humidities at moderate temperatures (28°) seem to cause the species to drink more water, while at the same time, due to the increased evaporation, there will be less water available in the vegetation or otherwise in the habitat of the species. The low air humidity and the lack of available water are, of course, closely correlated with the amount of rainfall.

No experiments were performed to determine the effect of different rates of air flow. It may be that a high rate of air movement would increase the amount of water needed by the animals. At least the high winds prevailing to the west of the range of the species assist in drying up the vegetation and thus are probably indirectly a factor in limiting the western distribution of the species.

The species is closely limited in distribution to the grassland habitat. This restriction in habitat is probably due to psychic reactions of some sort, and is evidently not due to an inability of the species to endure the climatic conditions in the forest.

The eastern limits of distribution of the species is evidently due to its limitation as to habitat. East of its range there were few native prairies and the species is seldom found anywhere except on prairies or in open fields. As the land to the eastward becomes cleared it is likely that the range of the species will be extended in that direction.

## Summary

The forest deer mouse, *Peromyscus leucopus noveboracensis,* has its habitat in the forest, while in the same areas, throughout a large part of its range in the Mississippi Valley, the prairie deer mouse, *Peromyscus maniculatus bairdii,* inhabits the open fields. The above-described experiments fail to find differences between the two species in their requirements for water, food, temperature, or air humidity sufficient to be the basis of these habitat differences.

The southward distribution of the prairie vole, *Microtus ochrogaster,* is possibly limited by the occurrence in its immediate environment at any time of a temperature in excess of 36° C. Its western limit of distribution is probably determined largely by the fact that the species must be excluded from areas in which the vegetation on the prairies sometimes completely dries up. Its eastward distribution under native conditions was probably limited by the dropping out of the prairies.

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# ECOLOGICAL FEATURES OF GREAT BAY, NEW HAMPSHIRE, AND A PRELIMINARY CHECKLIST OF ITS FISH

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For a number of years the writer has been collecting data on the distribution of the vertebrates of New Hampshire. Particular attention has been given to the relative number of individuals, and an attempt has been made to determine the ecological factors governing the abundance of certain species of fish.

During this work considerable variation in abundance from one time to another has been noted. The following checklist of the fish of Great Bay, New Hampshire, includes the five-year period from 1915 to 1920. The cause of fluctuations in numbers will not be analyzed in this paper, although a detailed study is being made of this problem.

The checklist includes the fish from Great Bay and Piscataqua River, above what is known as the Dover Point Bridge. This body of water is approximately seven miles long by about four miles at its greatest width, and is connected with the Atlantic Ocean at Portsmouth, New Hampshire, through the Piscataqua River. It receives a large number of streams, the most important of which is the Exeter River, Lamprey River, Oyster River, and the Bellamy River, as well as six or eight brooks of comparatively small size. The following points of ecological importance should be noted:

## 1. The Character of the Shore Line

The shore line of Great Bay is exceedingly indented. Numerous rocky promontories of from 50 to 150 feet in height form an almost unbroken series of small coves and inlets. The granitic character of the shore line is such that but a small amount of silt and soil is washed into the waters of the bay. The material, therefore, which goes to make up the extensive mud flats and the silt bottoms of the coves is for the most part of a finely divided nature and has been transported from a considerable distance by the rivers and streams.

The small coves furnish an excellent habitat for such groups as *Fundulus,* the Gasterosteidae, and similar shore-inhabiting forms. In but two or three places along the shore are there extensive swamp areas, since the silting in of the small bays and inlets has not as yet proceeded to the swamp stage.



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## 2. Types of Substrata

It would be difficult to find a greater variation of substrata than exists in this area. Many local studies have been made, which are, however, too much in detail to be included in this report. A few typical sections will serve to show the great variation in environment.

*Section A.*—From Cedar Point, at the mouth of the Bellamy River, due south to the deepest indention of Broad Cove. This section, approximately one mile long, includes roughly the following environmental conditions:

Beginning with Cedar Point, one passes within a few yards from a boulder-strewn shore at the high-tide mark through the sub-boulder, stone, gravel, sand, and hard clay deposits, all of which sections are more or less affected by the waves at the various tide levels. The mud-flat which follows the hard clay deposit extends out for some 250 yards and is densely covered with *Vallisneria.* This forms an ideal habitat for the *Fundulus,* pipe-fish, the eel, and the sticklebacks, which find not only protection but an abundance of food under the long-matted strands of the eel grass.

This zone, however, furnishes only temporary protection, for at low tide the greater part of it, except very small tidal pools, is exposed for one half to three quarters of an hour. *Fundulus* when caught in such a locality by the receding tide burrows into the soft mud of the pools and remains until the tide returns. This habit may also be noted in some other forms, such as the eel and occasionally in a small flounder.

By far the greater number of fish retreat with the last of the tide and find shelter in the eel grass at the edge of the mud-flats. Here congregate all of the larger predaceous fish, such as the whiting, pollock, and an occasional cod, to feed on the abundant life of the flats which temporarily collect along the margin. At the edge of the channel the flats drop off abruptly to a depth of from 25 to 45 feet to the clay bottom of the river. The surface is usually hard and smooth, being scoured by both the flow and ebb of the tide.

Over this vast expanse, which at this point is about three fourths of a mile wide, may be found numerous sculpins, flounders, and skates.

As one approaches Broad Cove there is an abrupt rise to the mud-flats, with practically a repetition of the conditions which prevail at Cedar Point. There is, however, this variation—the mud-flats of Broad Cove are never entirely exposed even at the unusual ebb tide in the fall and spring.

*Section B.*—From Foxes Point to Half-Tide Rock a line may be drawn northwest which, within the distance of three quarters of a mile, passes through a much greater variety of substrata. At Foxes Point one first encounters a flat of fine sand always covered with at least 3 feet of water. Here and there are to be found clumps of *Vallisneria* with an occasional boulder covered with a great variety of sessile forms.

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At this point, except for one half hour at the ebb and flood, there is a swift current running first in one direction, then in the other. Just off this flat the substratum drops to about 35 feet in what amounts to a large eddy due to the nature of the ledges above and below. Here the substratum is of small stones and boulders, with occasional clumps of *Vallisneria* on the shallower slopes near the shore. In this locality may be found a greater variety of fish than in any other; nearly all species have been taken from this pool except the smaller forms such as *Fundulus* and Gasterosteidae.

Here are found cunners (*Tautogolabrus adspersus*) in the greatest abundance and, in season, the cod, pollock, frostfish, and whiting, while on the small sandy or clay patches of the bottom are flounders, sculpins, and skates.

Passing from this area outward the current becomes swifter as it flows over the rocky ledges in midstream. At places these rocks lie just below the surface, while near by they may drop to forty, fifty, or even sixty feet of water. Everywhere these rocks are covered with the long fronds of the various species of kelp, which serve as protection for numerous shrimps and crabs.

As one approaches Half-Tide Rock, opposite the mouth of Oyster River, the rocky ledges give way to a small strip of hard sand in about thirty feet of water. This area is known as the "Cod Grounds" and here collect in the late fall and early spring a considerable school of codfish ranging in weight from six to fifteen pounds. Here also may be found numerous cunner of quite large size, as well as sculpins, flounders, and an occasional skate.

From this area the substrata rises abruptly to Half-Tide Rock, which, as its name implies, is only submerged as the tide is near flood. From Half-Tide Rock to shore, a distance of about two hundred yards, the surface is strewn with boulders and clumps of *Vallisneria,* with frequent tidal pools at low tide.

*Section C.*—A section at any point through Great Bay proper would pass through an endless succession of mud-flats exposed at low tide. These flats are densely covered with *Vallisneria,* except in restricted areas, and are traversed by numerous channels. The channels are about thirty yards across and from ten to fifteen feet in depth with a hard, even, mud bottom. But few forms of fish are found in this area except the pipefish and flounder and wandering schools of *Fundulus,* although the channels are used as thoroughfare for those forms which pass into the various rivers emptying into Great Bay.

### 3. Invertebrate Life

Only the briefest summary can be given of the invertebrate life of Great Bay. The list includes all of the species common to this section, some occurring in great abundance. This is particularly true of the shore line and the eel grass beds which are literally teeming with shrimp, while the rocky

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bottom of the deeper portion (Section B) furnishes an environment well suited to a variety of crabs which are found in large numbers. During the spawning season great schools of *Nereis* are to be found as well as a liberal supply of other worms.

A summary of the checklist of the invertebrates, exclusive of the Protozoa, follows:

| | |
|---|---|
| Porifera | *Cliona sulphurea.* |
| Coelenterata | Seven species. |
| Polyzoa | Two species. |
| Worms | Ten species, of which *Nereis* is the most abundant. |
| Echinodermata | Eight species. |
| Bi-Valve Mollusca | Seven species, of which *Mya, Modiola, Ostrea* are the most abundant. |
| Uni-Valve Mollusca | Fourteen species, of which *Littorina, Ilyanassa,* and *Melampus* are the most abundant. |
| Barnacles | *Balanus improvisus.* Very abundant on all channel rocks. |
| Schizopoda | *Michteimysis stenolepis,* quite abundant. |
| Isopoda | Four species. |
| Amphipoda | Twelve species. |
| Decapoda | Seven species. |
| Xiphosura | *Limulus polyphemus,* everywhere abundant. |

This summary includes a total of seventy-five species, many of the most important forms from the standpoint of fish food, being very abundant.

It would seem that almost ideal food conditions exist for a great variety of fish, especially if the enormous number of *Fundulus* in any suitable locality is considered.

## 4. Water Conditions

*A. Salinity.*—The water of Great Bay is of the usual brackish type. Owing to the considerable flowage from the rivers there is marked variation in the salinity from time to time. There is a considerable drop during the spring freshets, the specific gravity reading as low as 1.000 at the surface, while in midsummer when the streams are low it may rise to 1.0245. Corresponding readings have not been taken from the Atlantic off Portsmouth Harbor except in July and August, when the average of ten readings on different dates was 1.0270.

It is unfortunate that more data could not have been secured on the oxygen concentration at different seasons and under varying tidal and flood conditions. The relation of this subject to the number and distribution of fish must be deferred to a later date.

*B. Temperature.*—Fluctuations in temperature of the waters in Great Bay are much greater than those of the ocean. During the winter months from the first of November to the latter part of February the temperature

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remains quite uniform. All of Great Bay proper, the rivers and coves freeze over, the thickness of the ice varying from a few inches to eighteen or twenty. The channels, however, in the Piscataqua River and the "tide rips" at the mouth of the bay seldom freeze over. During the summer, owing to tidal flow and to the fact that numerous ledges occur in the bottom of the channel, the temperature is quite uniform from the surface downward. In July, August, and the first part of September the average temperature is from eight to ten degrees higher than that of the Atlantic Ocean off Portsmouth Harbor. At the same time it is considerably lower than that of the rivers which flow into it.

*C. Tidal Flow.*—Except for from thirty minutes to an hour during the turn of the tide the water of Great Bay is in continuous movement. The tide rises on an average of about nine feet, although during the high autumn and spring tides the rise is very much greater.

As a considerable area must be covered by each incoming tide, the current at the mouth of Great Bay where it flows through the Piscataqua River to and from the Atlantic is very swift. Owing to the ledges which intercept the bottom of the channel, "tide rips" are formed with extensive whirlpools and surface agitations. The roar of the water on occasions may be heard for one half to three quarters of a mile. In other localities extensive whirlpools are formed of comparatively slowly moving water. The fish which visit this area may therefore find the greatest variety of currents as well as variation in other environmental conditions.

*D. Impurities.*—Owing to the proximity of several villages as well as the cities of Dover and Portsmouth, considerable sewage is poured either directly or indirectly into the waters of Great Bay. The amount of this material which actually reaches Great Bay is difficult to determine. Probably the greater percentage of solid matter is deposited on the mud-flats of the streams before they empty into the bay. At the same time the chemical constituents of the water must be affected.

## 5. Limiting Factors in the Distribution of Fish

The factors determining the number of species can not be fully presented in this report. It is quite evident that a radical change has taken place within recent years.

Commercial fishing, which has played such an important part in the abundance of fresh-water fish, can not be considered as a factor in this region. At no time has there been extensive commercial fishing. This applies not only to the waters of Great Bay and its tributaries, but also to the waters of the Atlantic adjacent to Portsmouth Harbor. As far as man is concerned, perhaps the chief limiting factor has been the damming of practically all the rivers emptying into Great Bay. This, as in other New England

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streams, reduced and ultimately stopped the run of Atlantic salmon, which have not occurred in this region for a number of years. Although the Lamprey eel is still quite abundant in certain years, the run is only a fraction of what it formerly was. Other important food species in addition to the Atlantic salmon which were formerly abundant, but which have now disappeared, are:

| | |
|---|---|
| Common sturgeon | *Acipenser sturio* |
| Shad | *Alosa sapidissima* |
| Mackerel | *Scomber scombrus* |
| Bluefish | *Pomatomus saltatrix* |
| Striped bass | *Roccus lineatus* |

This change in habits can not be due to the lack of food material, for, as has been shown, there is still an abundance of food of all kinds. A careful analysis of the factors governing the distribution in Great Bay will be given in a later paper.

## 6. Checklist of the Fish of Great Bay

The following is a checklist of the fish of Great Bay known to have occurred within the five-year period from 1915 to 1920:

1. **Petromyzon marinus** Linne. Lamprey.
   Occasionally common in the spring below dams at head of brackish water.
2. **Raja erinacea** Mitchill. Little skate.
   Fairly common.
3. **Anguilla rostrata** Le Sueur. Common eel.
   Very abundant at the head of brackish water. The only species of fish caught for commercial purposes.
4. **Clupea harengus** Linne. Labrador herring.
   Usually common in the colder months.
5. **Pomolobus pseudoharengus** (Wilson). Alewife.
   Very common in the spring at head of tide water.
6. **Brevoortia tyrannus** (Latrobe). Menhaden.
   Very rare.
7. **Osmerus mordax** (Mitchill). Smelt.
   Very common throughout the colder months at the head of tide water.
8. **Fundulus heteroclitus** (Linne). Killifish.
   Very abundant throughout the year.
9. **Pungitius pungitius** (Linne). Nine spined stickleback.
   Fairly common.
10. **Gasterosteus bispinosus** Walbaum. Two-spined stickleback.
    Fairly common.
11. **Apeltes quadracus** (Mitchill). Four-spined stickleback.
    Common.

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12. **Syngnathus fuscus** Storer. Pipefish.
Common along the shore.
13. **Poronotus triacanthus** (Peck). Butterfish.
Fairly common in the spring.
14. **Tautagolabrus adspersus** (Walbaum). Cunner.
Exceedingly abundant in summer around rocky ledges.
15. **Tautoga onitis** (Linne). Tautog.
Very rare.
16. **Myoxocephalus aeneus** (Mitchill). Pygmy sculpin.
Rare.
17. **Myoxocephalus groenlandicus** (Cuv.). Black sculpin.
Very common.
18. **Myoxocephalus octodecimspinosus** (Mitchill). Long-spined sculpin.
Very common.
19. **Hemitripterus americanus** (Gmelin). Sea raven.
Uncommon.
20. **Merluccius bilinearis** (Mitchill). Silver hake.
Occasional.
21. **Pollachius virens** (Linne). Pollock.
Occasionally common.
22. **Microgadus tomcod** (Walbaum). Tomcod.
Very common in the fall.
23. **Gadus callarias** Linne. Cod.
Locally common in the spring and fall.
24. **Urophycis tenuis** (Mitchill). Squirrel hake.
Found occasionally.
25. **Pseudopleuronectes americanus** (Walbaum). Winter flounder.
Very common.
26. **Liopsetta putnami** (Gill). Smooth-back flounder.
Common near head of tide water.
27. **Lophius piscatorius** Linne. Fishing frog.
Very rare.

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# THE SEASONAL DISTRIBUTION OF THE APPENDICULARIA IN THE REGION OF SAN DIEGO, CALIFORNIA

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Though microscopic or almost microscopic in size, appendicularians rank rather high in the evolutionary scale because of their alliance with the chordates, and have peculiar interest on account of their structural resemblance to certain elementary stages in development of vertebrates. Unlike sedentary tunicates which lose their tails and notochords in adult life, the appendicularians retain these structures permanently. Hence it has often happened in the past that observers have regarded them as larval forms of sedentary species. Now, however, it is well known that they constitute a distinct group, containing many genera and species, all of which are pelagic. As early as 1896 Lohmann had described eight genera and thirty-four species.

Appendicularians are pelagic tunicates belonging to the class Copelata and to the order Archipneusta. This order contains two families: Kowalevskidae and Appendicularidae. The former consists of a single genus and a single species, while the latter includes all other recorded genera and species. Since the first-mentioned family (Kowalevskidae) is rarely represented in this vicinity, it is not discussed in this paper. Discussion of the other group is undertaken under the name Appendicularians because all the past literature has appeared under the designation of Appendicularia.

The shape of an appendicularian is somewhat like that of a hammer, the short, stout body in place of the hammer head, and the long, broad tail in place of the handle. The tail is attached to the ventral side of the body at right angles and somewhat toward the posterior end. This tail, besides being the bearer of the notochord, serves also as a powerful organ of locomotion, propelling the body by its vibration.

Like all other tunicates, the animal is partly inclosed by a cellulose tunic, usually called "house" in these forms. This structure is enormously developed in all species in certain regions (mainly colder), so that not only the anterior part but the whole animal may be inclosed in it. With one exception, all species are hermaphroditic.

This paper aims to give only certain points of ecological interest concerning appendicularians, while anatomical and taxonomic features are reserved for a monograph on Pacific Coast Appendicularians, which the writer has almost ready for publication. For convenience, taxonomic reference in this article will be mainly limited to the two sub-families, Oikopleurinae and



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Fritillarinae. The differences in the two groups are quite conspicuous, as may be easily seen by a glance at the accompanying figure (fig. 1).

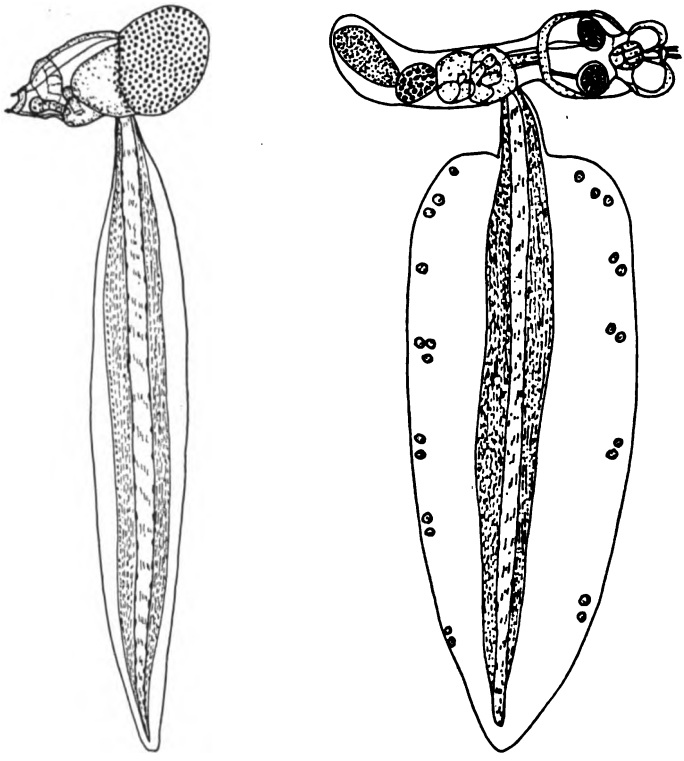

FIG. 1. Left *Oikopleura dioica;* right, *Fritillaria formica.*

Identification of species is much more difficult. Only occasional reference will be made to any particular species.

Continuous daily records of seasonal distribution of the two groups have been kept for some years, and by means of these it seems possible to identify certain interesting influences and tendencies in distribution.

Especially valuable contributions to our knowledge of distribution of appendicularians have been made by Lohmann (2) and Aida (1). At best, however, all such previous studies have been more diffuse or fragmentary than those here reported. Other studies have done little more than give geographical occurrence over wide areas, while these give an intensive view for one locality. Other conclusions have been based on very limited observations, often a single haul in each locality, but this work has been confined to a small area for a period of three years. Throughout this time daily collections have been taken from the surface of the water at or near the end of the pier at the Scripps Institution for Biological Research of the University of

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California at La Jolla, California. The results summarized in the following pages are based on continuous records of observations of this material.

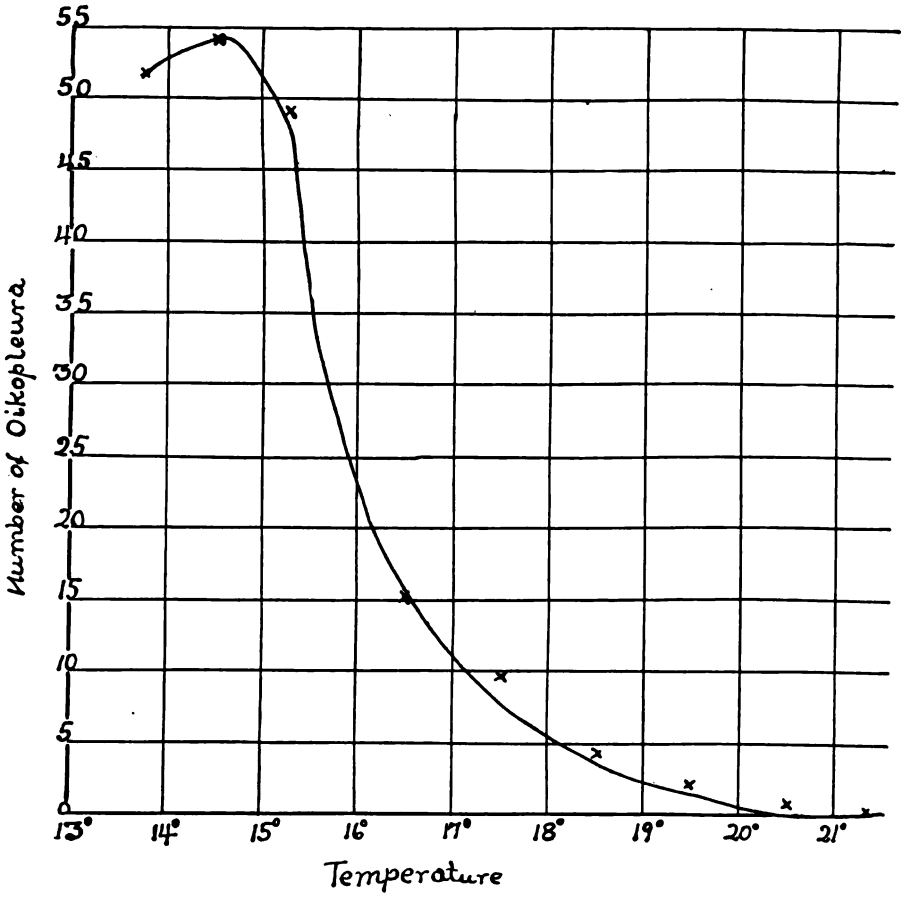


FIG. 2. Distribution of *Oikopleura* in relation to temperature of the surface water. June 1917 to March 1921.

These records show that the numbers of appendicularians are not uniformly distributed throughout the year. On the contrary, distribution varies widely with the seasons. Maximum numbers of individuals are to be found in winter, minimum numbers in summer. In fact, they are often entirely missing in warm weather. In general the data show a very marked correlation between the temperature of the water and the number of appendicularians, in which increase of temperature is accompanied by or followed by decrease in numbers and vice versa.

The average daily temperature and number of appendicularians for each month, covering the period of over three years, are given in Table 1, which

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gives the distribution of *Oikopleura* and *Fritillaria* in relation to temperature, and summarized graphically in figures 2 and 3.

These results point strongly to the conclusion that the distribution of appendicularians is sharply influenced by the temperature and by seasonal changes. The greatest numbers of species and individuals occur in the cooler

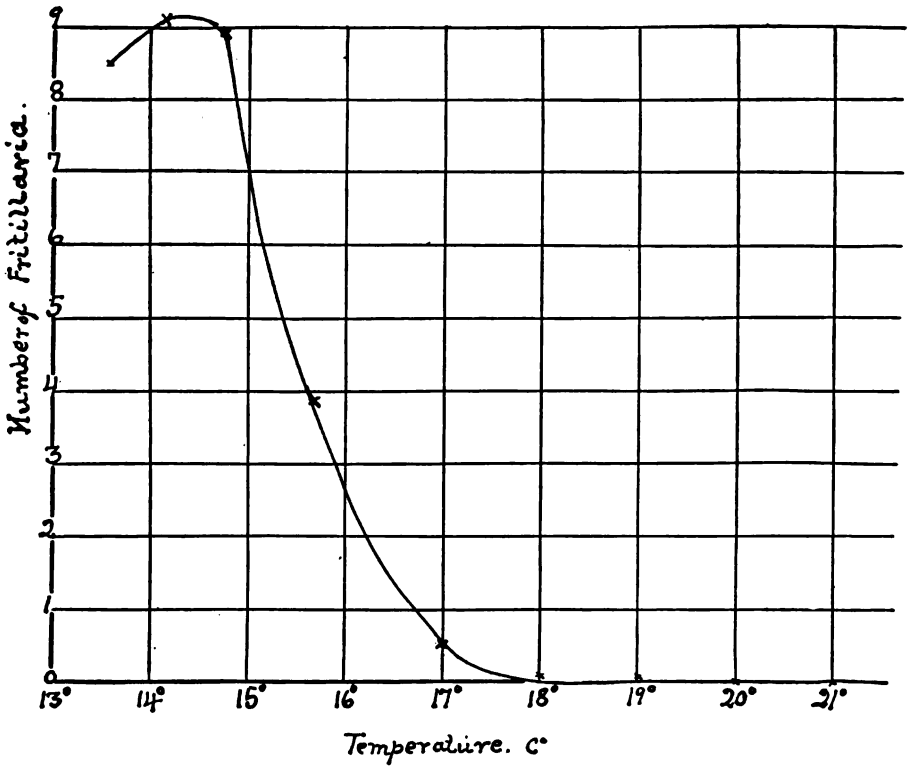


FIG. 3. Distribution of *Fritillaria* in relation to temperature of the surface water. June 1917 to March 1921.

months from October to March or April. After that the animals decrease in number gradually, until in the summer months the *Fritillaria* almost completely disappear from the surface waters, and only the cosmopolitan species of *Oikopleura* such as *O. dioica* and *O. longicanda,* with rare exceptions of other species, occur in limited numbers in that season.

As is shown in curves 2–3 and the table, the optimum temperature lies between 14° and 16° C. At this temperature the maximum representation is reached. In a temperature above 16° a decrease of appendicularians is noticed, and at 20°–22° they are almost completely absent from the surface waters. This is especially true of *Fritillaria,* which disappears from the surface in March or April and reappears again the following autumn in October or sometimes in the latter part of September, and is then quite abundantly

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TABLE I. *Average daily temperature and number of appendicularians from June, 1917, to March, 1921*

| Months | 1917–1918 | | | 1918–1919 | | | 1919–1920 | | | 1920–1921 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. of *Oikopleura* | No. of *Fritillaria* | Temperature of surface water, Degrees C. | No. of *Oikopleura* | No. of *Fritillaria* | Temperature of surface water, Degrees C. | No. of *Oikopleura* | No. of *Fritillaria* | Temperature of surface water, Degrees C. | No. of *Oikopleura* | No. of *Fritillaria* | Temperature of surface water, Degrees C. |
| June | 2.8 | 0 | 18.8 | 4.7 | .087 | 19.9 | 2 | ..... | 18.78 | 4.8 | 0 | 19.5 |
| July | 2 | 0 | 21.3 | 1.95 | ..... | 21.3 | 1 | ..... | 21.9 | 3.2 | 0 | 19.03 |
| August | 5.3 | ..... | 21.5 | 0 | ..... | ..... | 2.9 | ..... | 20.5 | 2.5 | 0 | 21.13 |
| September | 4.5 | ..... | 19.7 | 2.7 | ..... | 21.8 | 5 | ..... | 18.4 | .05 | 0 | 18.83 |
| October | 6.5 | .3 | 17.9 | 5.8 | .26 | 19.65 | 13 | .07 | 18.3 | 20 | 1.5 | 16.97 |
| November | 21.7 | 7 | 16.3 | 24.6 | 1.56 | 17.3 | 65.6 | 3.05 | 15.9 | 115 | 6 | 15.22 |
| December | 37 | 1.8 | 15.5 | 52.3 | 10.84 | 14.9 | 20.7 | 8.8 | 14.5 | 95 | 2.6 | 13.62 |
| January | 38 | 2.4 | 13.7 | 61.7 | 17.5 | 14.45 | 51.1 | .7 | 13.87 | 75.5 | 9.2 | 13.38 |
| February | 46.5 | .9 | 13.6 | 73.8 | 28.5 | 14.08 | 15.6 | 8.0 | 14.2 | 16 | 3.5 | 13.11 |
| March | 15 | ..... | 14.6 | 167.2 | 18.2 | 13.75 | 77.8 | 11.2 | 14.4 | 16.7 | 2.1 | 14.25 |
| April | 89.8 | ..... | 15.4 | 50.6 | 6.2 | 14.75 | 42 | .03 | 14.7 | ..... | ..... | ..... |
| May | 16.3 | ..... | 17.9 | 18.7 | ..... | 17.4 | 10.5 | 0 | 16.21 | ..... | ..... | ..... |

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represented during the colder season. Only once during the three summers covered by the observations did *Fritillaria* occur. This was on June 14, 1918. The temperature of the water had suddenly dropped from 19° to 16°. That day the *Oikopleura* were very numerous considering the season, and among them were found two *Fritillaria*. Whether it was due to the upwelling of cold waters or to some lateral current that the temperature fell so suddenly is not certainly known, but undoubtedly the same cause that brought about a change of temperature was also responsible for the increase of *Oikopleura* and for the appearance of *Fritillaria*. It indicates that the animals dwell in either deeper water or in colder regions of higher latitudes during the hot summer months.

Reading the averages in the tables, one may get the idea that the appendicularians are equally distributed throughout the month or the season. This, however, is not the case. On the whole, species and individuals of *Oikopleura* and *Fritillaria* occur in greater abundance during the winter season, but not all the species are equally represented at the same time, various species being more prevalent than others at different times. For instance, as many as 200–300 individuals of *Fritillaria formica* in a catch were taken several days in succession. Then that species disappeared completely and has never again been taken in such abundance. Similarly other species have predominated at different times. *Oikopleura fusiformis* occurs frequently and suddenly in unusually large numbers (100–200 or more in a catch). It, too, disappears sometimes as suddenly as it appeared. The same is true of many other species. They seem to come and go sporadically, with the only difference that some species are comparatively rare and never occur in such large numbers.

One such rare species is *Appendicularia cicula*. It is seldom found in this region, hence during the first year of investigation none appeared. In the second winter three specimens were found in different catches. The last two winters it has been found again occasionally, but always in very limited numbers; two per catch has been the largest number thus far. *Appendicularia cicula* has been reported as being present in all tropical waters. It occurs in great abundance near the estuary of the Amazon River and off the West Coast of Africa, in the region of Sierra Leone. According to Lohmann, this species is usually found in surface waters in a temperature of 16°. On the African Coast, where the surface temperature is about 29.5° C., *Appendicularia cicula* dwells in deeper waters at a temperature of 11°–18°.

Kowalevskia was not found in this region until December, 1920, when five specimens of that group were taken in three different hauls within a period of four days. It has not been seen since that time. *Fritillaria pellucida* was recorded for the first time in this region in January, 1921. Only two specimens of it have been seen here thus far.

A good many other species appear more or less abundantly and irregu-

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larly at different times, so that it is impossible to know or to predict their coming or going in advance. Even the most common species of this region, such as *Oikopleura dioica* and *O. longicanda,* may appear suddenly in unusually large numbers, only to disappear again gradually or as suddenly as they came. Thus it happens that the average number of *Oikopleura* recorded as 1–2 per day, during some summer months, is not literally true, but the number was probably zero per day for the greater part of the time, the average being obtained from relatively large catches in one or two days of the month. The most satisfactory way to deal with the records would be to include the complete data here; but since that would occupy too much space, one must be content with a general idea of distribution obtained by comparing the average number of each month and season as summarized in the tables.

The aforementioned facts prove the necessity and importance of long and continuous observations on distribution. Were it not for such observation, some species would not have been discovered in this region, while others would be recorded as being abundant, especially if judged from a single catch that happened to contain an exceptionally large number of the species. Such exceptional cases are apt to lead the observer to erroneous conclusions. On the other hand, comparisons and observations of numerous collections taken from a locality regularly tend to reduce such errors, and the average data thus obtained give one a fairly good idea concerning the distribution of certain animals in a locality.

The lack of uniformity in distribution, and sudden appearance and disappearance of large numbers, leads to the question as to the explanation or cause of such conditions. Since it is impossible to follow these microscopic creatures in the vast body of water to obtain first-hand information, one may at least make a scientific guess as to what the possibilities may be.

Undoubtedly appendicularians are in existence somewhere else when they are not in the surface waters near the shores. A fair supposition is that when the temperature of the surface waters here becomes too warm the animals migrate either downward to deeper layers where the temperature is lower, or die off here while continuing to live in the surface waters of higher latitudes. One of the reasons for the uneven distribution of the different species may be that each has its particular period of reproduction. If the conditions for the development of the eggs and the young are favorable, a species may become very abundant in a locality and may be suddenly drifted to some other place by a passing current. Very little is, as yet, known about the local currents, but one has only to observe the ocean on a few calm days when their course can be seen to some extent to appreciate their importance in the distribution of the pelagic fauna.

Although no daily, continuous observations have been possible on the vertical migration of the appendicularians, a few hauls taken from deeper waters of this region in summer indicate that the animals are more abundant

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in deeper layers than at the surface during that season. However, these facts need more positive proofs and a more careful, systematic study.

That the distribution of appendicularians does not depend entirely on the season or the time of the year was found by a comparative study of the daily catches taken from the pier here at La Jolla and surface collections made in tropical seas at the same time, from February to April, 1920. These surface collections were made by W. C. Crandall and E. L. Michael from the yacht *Kemah* on a run from Jacksonville, Florida, to San Diego, California, by way of the Panama Canal. It is much regretted that no deep-water hauls could be taken on this trip. However, about 500 surface hauls were taken. Although appendicularians were very abundant in the surface waters of the San Diego region when these hauls were taken, they seemed to be almost completely absent from the surface of the tropical seas. However, allowance has to be made for the fact that the samples from the vessel were only about two percent as large as those from the pier. The temperature at the surface of the tropical waters varies from 16° to 29° C. Out of the 170 tropical surface hauls taken during the latter part of February and the early part of March, only thirty contained some *Oikopleura,* about 1 to 2 specimens per haul, except in 8 successive hauls, which reached fifteen to sixty per haul. *Fritillaria* were completely absent from all the hauls. Of three hundred and thirty hauls in Pacific waters, two hundred and seventeen contained appendicularians. Their number was very low in the hauls from the warmer tropical waters, but increased considerably with further advance northward into cooler waters until near San Diego, where the temperature was 14°–15°, *Oikopleura* were 100–150 per haul. From all five hundred hauls only seventeen contained some *Fritillaria.* These were all from the colder waters of higher latitudes, none being from tropical waters. Lohmann mentions some of the tropical localities traversed also by W. C. Crandall and E. L. Michael as having no *Fritillaria* in the surface waters, but he says they were abundant at a depth of 100–200 meters.

The above observations suggest that appendicularians live in surface waters as long as the temperature and other conditions are favorable for their existence, but when the temperature rises too high they seek the cooler waters in greater depths. How these animals find their way downward is unknown. Maybe by a trial and error method as Jennings found in his experiments with Paramecea. Or it may be that with the rising temperature the animals become positively geotropic and negatively phototropic, and thus move downward. In low temperatures these tropisms may be reversed and an upward movement take place. However, there is no positive proof for any such hypothesis. Some laboratory experiments on the positive and negative tropisms of the appendicularians would be of great interest if the extremely delicate condition of these animals did not render them almost entirely unfit for such experimentation. Every attempt to do experimental work with

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the creatures has thus far met with failure. As far as my observations go, the appendicularians do not show any tendency toward positive or negative phototropism, and when left in a dish in diffused light they do not gather on the window-side of the dish nor on the opposite side, as do many other animals with pronounced positive and negative tropisms, but remain scattered in the dish, moving in various directions.

Slight changes in light intensity do not seem to have any immediate effect on their distribution. They may be abundant in the surface waters on a bright, sunny day as well as on a cloudy or foggy day; or they may be very scarce or absent under either of those conditions. Of the few conditions under observation, the temperature seems to be the most important factor, having an immediate effect on distribution.

Next to temperature, the microplankton is to be considered as having influence of some importance, for the food of appendicularians consists of minute Protozoa, bacteria and other organisms of the kind. The water sample from the tropical regions not containing any appendicularians were also apparently void of any other organisms, so that the absence of food as well as the high temperature may be responsible for the absence of these tunicates in the surface waters. On the other hand, an excess of some of the microplankton organisms may be the cause of the disappearance of all appendicularians from the surface waters. It happens at times that such phytoplankton appears suddenly in such abundance that the water is thick and has a green or brown color and a disagreeable odor. On the first day of the appearance of this condition the appendicularians may be quite numerous, but they are sluggish, dead, or in a dying condition when they arrive at the laboratory. If the microplankton continues to exist in abundance for several days in succession, the appendicularians disappear completely from the hauls until the water is in a normal condition again. Evidently there is some poisoning effect produced by the great abundance of such microplankton in the water which exterminates the appendicularians.

Various predatory animals may be responsible for the decreasing numbers of appendicularians. As such, some of the small forms of Medusae have been frequently observed. If the latter appear in abundance with the former, medusae can be seen under a microscope attacking the appendicularians. The attack is usually begun at the tail end, and the victim is held tenaciously until the whole animal has been devoured. Similar attacks are made by Copepoda and other animals, although not so frequently. However, these are only a few of the facts that have incidentally come under my observation in the laboratory. Most of the conditions existing in the natural surroundings—the ocean—are beyond one's power of direct observation.

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## Summary

1. The numerical results of an intensive study of appendicularians prove conclusively that the distribution of these tunicates is closely related to temperature, and that the number of individuals and species increases as the temperature decreases, and vice versa, until the optimum temperature 14°–15° C. is reached.

2. In this region the distribution of appendicularians in the surface waters is sharply influenced by the seasonal changes. With a few exceptions of some cosmopolitan *Oikopleura,* which occur occasionally in the surface waters in summer, the greater part of *Oikopleura* and all the *Fritillaria* are absent from the surface waters during that season. But all species are more or less abundantly represented in the surface waters during the winter season between October and April. However, the rich surface distribution in the winter in the San Diego region may be due to the prevailing low temperature in that season. Surface hauls taken from the warm tropical waters in the winter months were either completely devoid of appendicularians or contained very few of them, showing a condition similar to that of the summer season in this region.

3. Some past observations point to the conclusions that appendicularians migrate downward and dwell in deeper waters when the surface temperature rises too high and is unfavorable for their existence. They come back to the surface again when the temperature drops lower. These scanty observations, however, have not been verified by any intensive systematic studies.

4. Laboratory experiments on the behavior of appendicularians have been almost impossible on account of the delicate condition of the animals. But as far as laboratory observations go these tunicates do not reveal any tendency toward positive or negative phototropism. The only satisfactory results have been thus far obtained from observations in nature.

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# INFLUENCE OF CERTAIN SOIL FACTORS ON THE GROWTH OF TREE SEEDLINGS AND WHEAT[1]

BARRINGTON MOORE

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## Climate and Soils

The influence of climate upon plants and animals under natural conditions has received more attention than the influence of soil. Climate exerts the major control; without heat, moisture, and light the most fertile soil is useless. In the mountains of our West climate is so closely related to altitude that different climatic zones occur within short distances and give the impression that climate alone influences distribution. In general—of course there are exceptions—those who have studied the environment of western American plants and animals have devoted most attention to climate, while those who have studied in the eastern United States and Europe have considered the influence of geological formation and soil as well as of climate.

Progress in studies of the relation of soil to natural vegetation has been slow, partly owing to the complexity of the problem, and partly because of insistence on the control exerted by physical properties of the soil to the exclusion of its other properties. But there are signs of change. Fernald's work (2) on the distribution of *Pinus Banksiana* and *Thuja occidentalis* has done much to emphasize the importance of geological formation. Hesselman's (4) investigations in Swedish forests have thrown much light on the importance of nitrogen in forest humus and on the influence of various kinds of humus and methods of treatment upon the composition and reproduction of the forest. His discoveries are of the utmost value and will stimulate work on soil factors.

[1] Presented before the Ecological Society of America at its meeting in Chicago on December 28, 1920.



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Humus has long been recognized as extremely important; in fact, the accumulation of humus in sandy soils has been considered sufficient to enable such soils to support the same kind of forest as that growing on the more fertile soils of the same climatic region. But, prior to Hesselman's work, the value of the humus had been attributed very largely, if not entirely, to its effect upon the water-holding capacity of the soil. It is known to render heavy soils lighter and better aired, and to make sandy soils less subject to rapid percolation and more retentive of moisture. Its influence has been considered almost wholly from the point of view of its effect upon the physical properties of the soil.

Soil reaction, acidity or alkalinity, is known to be of much importance, but most attention has been given to degree of acidity, with comparatively little study of alkalinity except for toxic salts in arid regions. It would be interesting to know the effect of alkalinity upon tree growth and whether certain trees are kept off of moderately alkaline situations by competition—or because they are unable to grow there.

## Experiment

An experiment was carried out in the summer of 1919 at Mt. Kisco, about 30 miles north of New York, to determine as far as possible (1) the influence of humus on tree growth, aside from its effect on the moisture-holding capacity of the soil, and (2) the influence alkalinity produced by slaked burnt lime (calcium hydrate).

From the point of view of fire protection alone, the influence of humus upon tree growth is important. Ground fires, such as those which frequently, often intentionally, run through hardwood forests and longleaf pine forests, destroy a certain amount of humus (3).

Lime is considered beneficial, so that any injury from lime should be due chiefly to alkalinity, although this is not absolutely certain, because it is probable that some trees do not thrive on lime soils which are neutral. The major part of the influence should, however, be due to the reaction.

In studying the influence of humus three soils were used, representing two extremes, absence of humus and pure humus, and an intermediate condition, a mixture of sand and humus. The first soil was pure sand, a rather sterile, fine, grey, water-worn, glacial sand, predominantly quartz, taken from about three feet below the surface of a glacial esker. The physical properties may be summed up by stating that the wilting coefficient, on the basis of air-dry weight, was .85 percent.[2] The reaction was neutral.

The pure humus, the opposite extreme of the pure sand, was a dark brown leaf mold not completely decomposed. It was collected from between crevices in a rock at the base of a cliff to insure a minimum of mineral soil. The

[2] The wilting coefficient figures throughout this paper are approximations, but serve to indicate differences in the physical properties of the various soils.

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rock itself was a granite, its decomposed particles underlying the humus and forming the only soil in the crevices. Almost none of these particles were included in the humus used. The forest which created the humus was of mixed hardwoods characteristic of moist rocky ravines in southern New York, Connecticut, and Pennsylvania (9). It contained white oak, *Quercus alba,* chestnut oak, *Q. prinus* (on the rockier places), red oak, *Q. rubra,* much sugar maple, *Acer saccharum,* black birch, *Betula lenta,* a little beech, *Fagus Americana,* a little shagbark hickory, *Hicoria ovata,* some white ash, *Fraxinus Americana,* and a scattering of dead chestnut, *Castanea dentata,* which had probably contributed its quota to the leaf mold. The reproduction was fairly abundant of chestnut oak, red oak, sugar maple, and white ash. Among the shrubs of the undergrowth was some laurel, *Kalmia latifolia,* viburnum, and a little dogwood, *Cornus florida.* Higher up the slope and about 50 to 75 yards away was a group of hemlock.

The wilting coefficient of this humus, on the basis of air-dry weight, was 43.5 percent. The acidity, determined by titration of an aqueous extract with .05 normal sodium hydroxide in the manner described by Coville (1) in his blueberry study, was .00114 normal at the start of the experiment, and was reduced by exposure from June 8 to September 12 to .00075 normal. By the Truog test (10), applied before exposure, it was between "medium" and "strong" acidity, nearly "strong"; after exposure this test revealed practically no change. Wherry's colorimetric method of determining the hydrogen and hydroxyl-ion concentration (11) had not been made available at the time these tests were carried out.

The intermediate soil was a mixture of the sand and humus above described in the proportion of 80 percent sand and 20 percent humus by volume. Owing to the lightness of the humus it made only 4 percent by weight and did not give the sand an appearance of a high humus content; in fact, it is probably somewhat lower than the surface layers under a typical forest of pitch pine. The addition of this amount of humus raised the wilting coefficient from .85 percent to 2.4 percent. The acidity became .001 normal before exposure and was of "medium" acidity by the Truog test.

In order to eliminate the effects of greater moisture-holding capacity, and to find the influence of humus on the nutrient properties of the soil, all soils were kept continually moist.

In the alkalinity tests a set of three soils, similar to the three above described except for the addition of lime, was used. The sand received 2 percent of air-slaked burnt lime by volume and the humus received 4 percent. The sand and humus received 2 percent of lime for the sand and 4 percent for the humus. It has been commonly supposed that burnt lime in the soil quickly absorbs carbon dioxide and assumes the neutral carbonate form. In a study of the comparative effects of burnt lime ($CaO$) and calcium carbonate ($CaCO_3$) on the soil reaction Hoagland and Christie (6)

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found that the burnt lime makes the soil strongly alkaline; this decreases greatly in 3 days, and after that more slowly, leaving the soils still alkaline after 10 months.

The alkalinity of these three soils was determined by titration with normal hydrochloric acid in .05 normal solution in the same way that the acidities were tested. The sand was .0058 normal alkaline at the beginning and was reduced to .00117 after 96 days' exposure. The mixture of sand and humus was .0036 normal alkaline at the outset and dropped to .00116 normal, or practically the same as the sand. The humus was very alkaline, .0127 normal at first and decreased to .00283 at the end.

A third series of soils, the same as the foregoing, but with a milder application of lime, was added on June 23, fifteen days after the other two series had been started. In this set the sand received only .75 percent of burnt lime: the mixture of sand and humus received .75 percent for the 80 percent of sand, and 1 percent for the 20 percent of humus. The humus received only .5 percent of lime. Titration tests showed that the sand had an alkalinity of .00127 normal at the beginning, which decreased to .00097 by August 29. The mixture of sand and humus was .00097 normal at the start; and the humus was only .00065 normal alkaline in the beginning and was neutral at the end. The alkalinity in this series was therefore comparatively low.

The addition of the larger amounts of lime appears to have slightly affected the physical properties. The wilting coefficient of the sand was reduced from .85 to .76 percent, and that of the sand and humus from 2.4 to 1.5 percent. The wilting coefficient of the humus was 50.2 percent with the lime, as against 43.5 percent without. With humus the lime caused the formation of a surface crust, due apparently to rapid carrying to the surface of water containing salts in solution, the water evaporating and leaving a crust of salts. This explanation would agree with Wolkoff's (**12**) work on the influence of alkali salts on soil moisture. The crust interfered with germination and re-formed as soon as broken.

The soils were placed in flats of cypress, *Taxodium distichum,* to avoid the influence of decaying wood. These flats were 8 centimeters deep inside, and 48 centimeters long by 37 centimeters wide. Each was filled level with the edge, but the humus settled with exposure more than the sand until it became about 5 centimeters deep as against about 7 for the sand. On June 8 each flat containing a soil as above described (except the light lime series) was sown with seed of red pine, *Pinus resinosa,* Jack pine, *Pinus Banksiana,* pitch pine, *Pinus rigida,* and white cedar, *Thuja occidentalis.* White pine, *Pinus strobus,* was also included, but did not germinate sufficiently to give results worth noting.

On June 10 five sugar maple seedlings one year old, of wild stock collected from the immediate vicinity, were transplanted into each of the six flats.

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On June 12 all flats received a row of marquis wheat kindly furnished by H. L. Shantz, of the Bureau of Plant Industry. The mild lime series was sown with the same species on June 23, except wheat, which was put in on June 24.

All flats were protected from birds and rodents by rust-proof wire netting with a 6 to 7 mm. (about quarter inch) mesh, since it had been found in previous work of this character that coniferous seed in unprotected flats is largely destroyed. Perhaps the flats attract curiosity and expose the seed to more danger than in a forest nursery. The wire cut off a certain amount of sunlight, perhaps about 20 percent or more; this was an advantage, since exposure to full sunlight is not beneficial to very young coniferous seedlings.

Measurements of the growth in height were made at about five-day intervals up to August 4, and then on September 12. The measurements were taken from the ground to the base of the cotyledons, and when the primary leaves appeared these were measured and their length added. The growth of the maple was taken by measuring the length of the primary leaves alone.

At the end of the season the growth of the roots for the entire period and the green weight of the seedlings were determined.

## Results

The results on the unlimed, strong lime, and mild lime series will be presented separately. The first series shows the influence of humus, and the second and third the influence of alkalinity and of lime in different proportions. The rate of growth is shown in the accompanying curves, figures 1, 2, 5, and 6, and the data on root growth and green weight is presented diagrammatically in figures 3 and 4.

### Influence of Humus

*Rate of Growth in Height.*—The rate of growth in height of each species has been plotted separately, but all three soils in the series are placed for comparison on the same graph. The results of the mild lime series have been included in the humus graphs for pitch pine, jack pine, and red pine, figures 1 and 2.

The differences shown are in no wise due to the effect of humus upon water relations, but upon the nutrient properties of the soil—its fertility. The physical properties of the soil do not enter into the problem except through effect on aeration, and in this series all the soils were porous enough to give abundant oxygen to the roots.

The favorable influence of humus shows strikingly. In spite of acidity there was far more rapid growth of all species on pure humus than on pure sand (see figures 1 and 2). The cause is almost certainly the nitrogen content of the humus and the lack of it in the sand. The nutrient value of

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humus and its influence on rate of growth in certain forests seems amply demonstrated.

Surface burning in a forest, by adding ashes to the soil, may stimulate growth temporarily; but, since it destroys the nitrogen which is seen to be such a large factor, and allows the remaining nutrients to be rapidly carried off by rain, its ultimate result must be to seriously check growth.

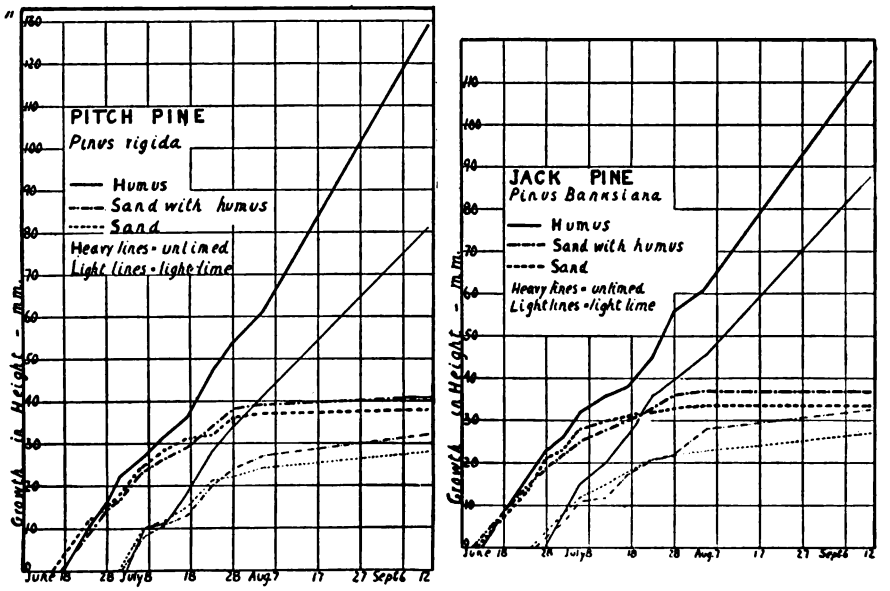


FIG. 1. On left, pitch pine seedlings, rate of growth in height on unlimed (heavier lines) and on lightly limed soils (lighter lines), showing the strong response to humus. On right, Jack pine seedlings, rate of growth in height on unlimed and on lightly limed soils, showing the influence of humus.

On the sand to which 4 percent of humus by weight had been added the growth rate was more rapid than on the pure sand, except in the case of cedar, which will be considered below. The difference in the growth of the trees on the pure sand and on the sand plus humus was not great, but distinct. It is interesting that the improvement produced by the addition of the humus to the sand, so far as trees are concerned, bore a closer relation to the proportion of humus in the sand by weight than by volume. The amount added by weight was small, 4 percent, and the increased growth of the trees was small. This would indicate that in forests the customary practice of measuring the percentage of humus by weight rather than by volume may be the better after all. The growth was, however, only that of a single season, a very short proportion of the life of a tree, and later growth might show the humus mixed with the sand to have a greater influence than that indicated by

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these curves. With wheat the influence of the humus added to the sand was greater than with the trees, and was more nearly in proportion to the volume of humus in the soil.

The favorable effect of the humus, either pure or in mixture, was not at once apparent. Germination was more rapid on the sand. If this was due to heat, it must have been on account of the smaller amount of water in the sand even at its optimum moisture content, and possibly to its greater con-

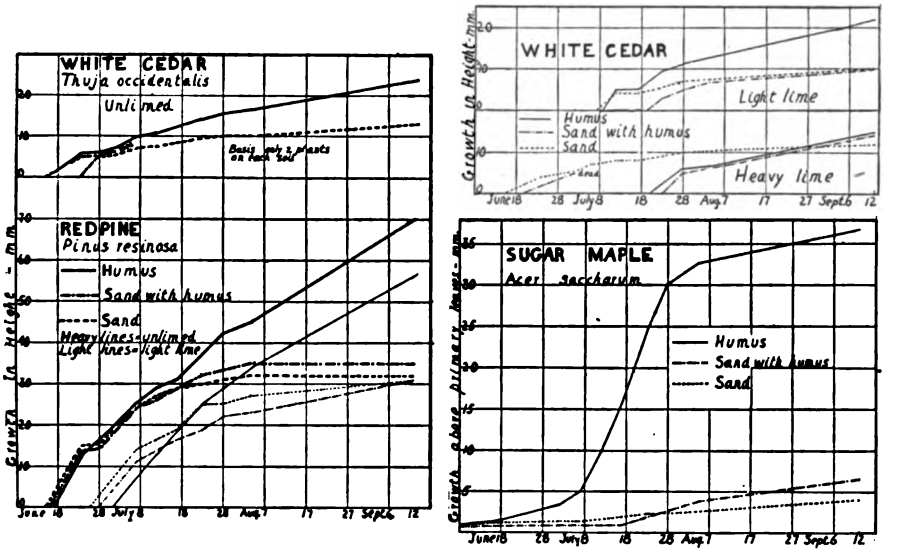


FIG. 2. On left, growth in height of white cedar (arborvitae) seedlings on unlimed soils; and of red pine seedlings on unlimed and on lightly limed soils; showing smaller response to humus on the part of cedar and red pine (compare with fig. 1).

On right, white cedar seedlings on lightly limed and on heavily limed soils. Shows later germination on heavily limed humus, and on sand with humus, but relatively less injury from lime than in the case of other species (compare figs. 1 and 6).

Sugar maple one-year-old transplants on unlimed soils, showing the influence of humus on the rate of growth in height above the primary leaves.

ductivity, for the sand was light colored and absorbed considerably less heat than the darker humus. It may be that the seeds absorbed water more rapidly from sand than from humus, because the humus was not thoroughly decomposed, and hence could not be packed as closely about the seeds as could the sand.

All species did better at first on the sand than on the mixture of sand and humus, but eventually those on the latter caught up with and passed those on the former; this occurred at about the same time for all trees. It may be that the nitrogen in the humus became available after a certain period of exposure.

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All species responded, but not equally, to the humus by a very marked increase in rate of growth. The response of Jack pine and pitch pine was considerably greater than that of red pine and cedar (see figs. 1 and 2). Jack pine and pitch pine are largely confined to the poorest and sandiest soils within their ranges. It may be that their strong response to humus is correlated with the character of the soil on which they ordinarily grow, and that they are able to persist on poor sandy soils because of this very ability, for there is always a considerable amount of humus mixed in with the sand of their natural habitat. The response of red pine and cedar to humus would be proportionally less than that of Jack pine and pitch pine, because they need other elements in the soil. It would seem that the greater the response to humus, the poorer the soil on which a coniferous species will thrive. Of course, the matter is not so simple as this, and will require much critical work on the availability of the various components of the soil solution, as well as on the physiological processes of absorption and metabolism, before any such law can be stated.

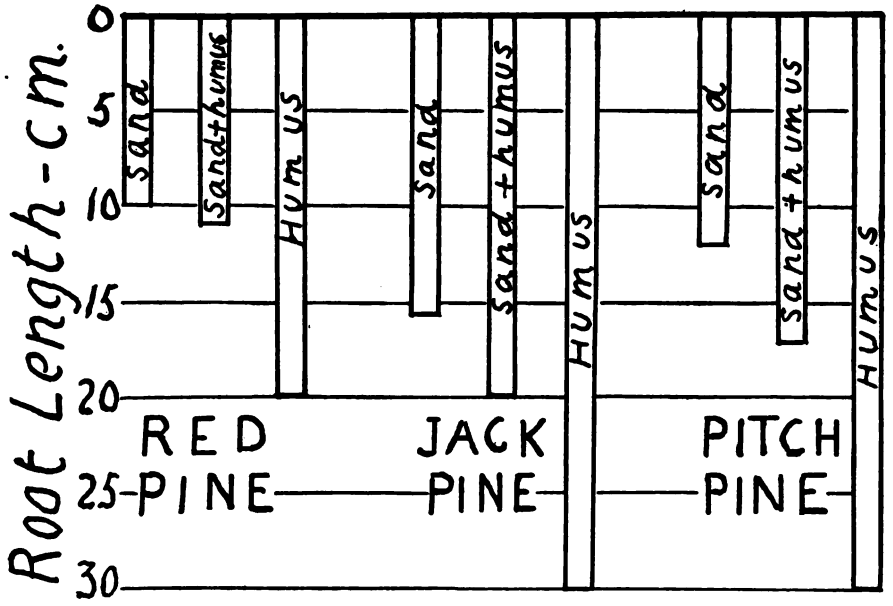


FIG. 3. Growth of coniferous seedling roots in length on unlimed soils, showing the influence of humus. Root area would have shown even greater influence.

Cedar, curiously enough, grew on the pure sand and on the pure humus.

The rate of growth fell off earlier in the season—by about July 8—on sand than on any other soil; on the mixture of sand and humus it diminished a little later, while on the pure humus a high rate was maintained by most species until the last measurement on September 12.

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but not on the mixture of sand and humus. The reason is unknown, unless it be that cedar will not tolerate acidity unless the acidity be compensated for by an abundance of humus. Fernald has shown (2) that cedar exhibits a marked preference for calcareous soils; the writer has found much cedar growing on Mt. Desert Island, Maine, where the soil was not calcareous, but contained abundant humus.

*Growth of Roots and Green Weight.*—The influence of the humus on root growth was as marked as its influence on height growth. The roots were not only longer, but more branched, and therefore had a much larger absorbing area than on the sand. In spite of the shallowness of the flats the roots on the humus attained lengths of from 20 to 30 cm., as against 10 to 13 cm. on the sand, and 11 to 20 cm. on the mixture of sand and humus (Table 1).

The effect on the growth of roots *in length* is shown in Table 1 and represented graphically in figure 3. This gives only part of the influence of humus, because it ignores the branches, and hence does not represent differences in total root area. Had it been practicable to measure the length of all the branches, the influence of humus would have been exhibited even more strikingly.

TABLE 1. *Growth of roots in length, unlimed soils*

| Species | Soil | | |
|---|---|---|---|
| | Average length, cm. | | |
| | Sand | Sand with 4% humus by weight | Humus |
| Jack pine | 13 | 20 | 30 |
| Pitch pine | 12 | 17 | 30 |
| Red pine | 10 | 11 | 20 |

The roots of Jack pine and pitch pine were longer than those of red pine, as would be expected from the drier and poorer soil in the native natural habitat of these species. It is not, however, safe to draw general conclusions as to the relation of depth of root to moisture and fertility requirements, because the response may be due to one of several factors, among which are not only moisture and fertility, but soil oxygen.

The influence of humus on green weight per seedling at the end of the growing season is given in Table 2 and shown graphically in figure 4. Although the difference between the pure sand and pure humus is very marked, the difference between the pure sand and the sand with 4 percent humus by weight, though distinct, is not very noticeable. The greater response which Jack pine and pitch pine make to humus, as compared with red pine, shows in the green weight as in the height growth.

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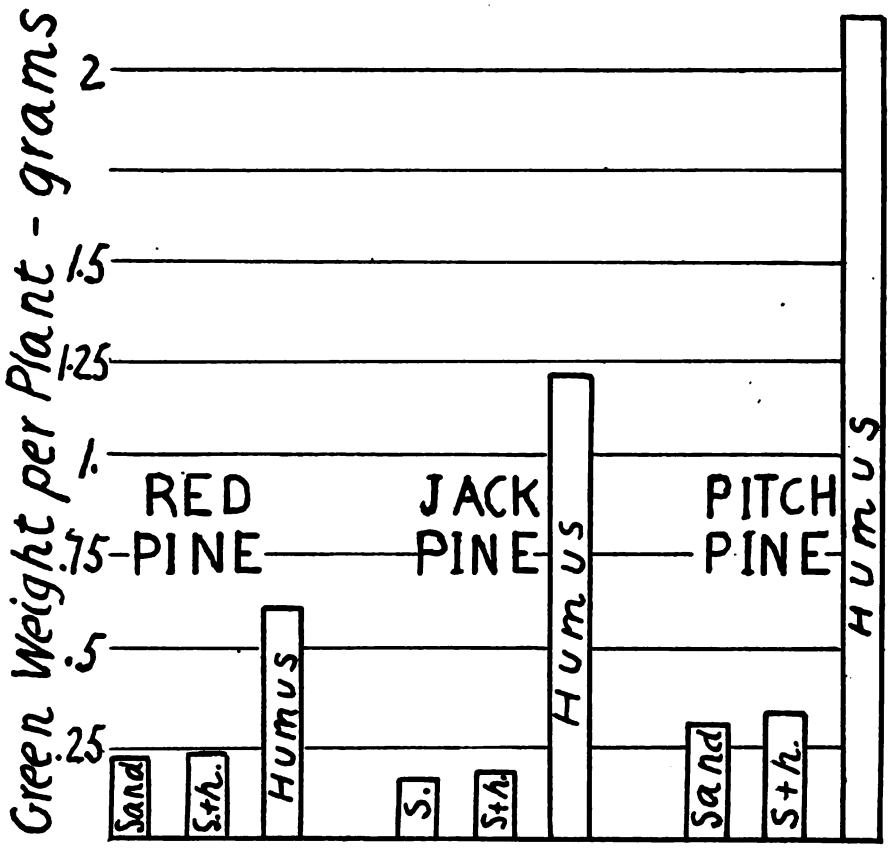


FIG. 4. Green weight of coniferous seedlings on unlimed soils, showing response to humus.

TABLE 2. *Green weight*

| Species | Soil | | |
|---|---|---|---|
| | Average green weight per plant, grams | | |
| | Sand | Sand with 4% humus by weight | Humus |
| Jack pine | .167 | .18 | 1.215 |
| Pitch pine | .31 | .34 | 2.14 |
| Red pine | .222 | .228 | .607 |

Pitch pine showed the greatest green weight, as well as the tallest height growth, and had a slightly more uniform growth throughout the season (see figs. 1 and 2). This may be because the climate was best suited to pitch pine, for it alone occurs naturally in the vicinity, or it may be merely a specific character.

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The effect of humus showed in the color of the plants, those on the mixture being slightly darker than those on the sand, which were a yellowish green, while those on the humus were bluish green, indicating greater thrift and vigor.

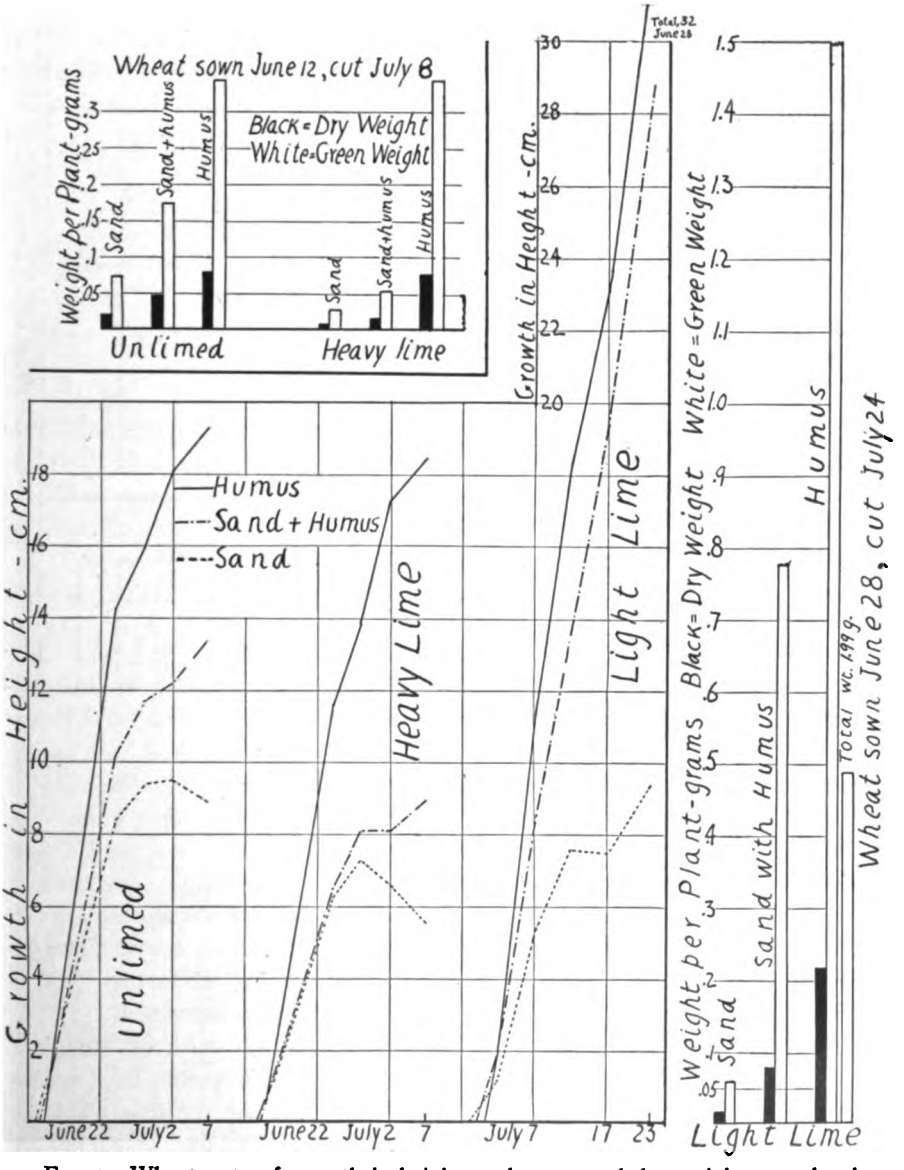


FIG. 5. Wheat, rate of growth in height, and green and dry weights, on the three soils of the three series. Green and dry weights are in upper left hand corner and on extreme right of figure. Shows less injurious effect of heavy lime as compared with coniferous trees (except cedar).

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*Influence of Humus on Wheat.*—The influence of humus on the rate of growth of wheat was very marked, although the proportionate increase on the humus was considerably less than in the case of the trees. Is this a further indication that plants requiring fertile soil respond less readily to humus than those which do well on poorer soil?

The period of growth was only 26 days, further growth on the humus being hampered by the wire screens. This is, however, sufficient with such a rapidly growing plant to show the influence of humus. At the end of the 26 days the plants on the sand were dying back at the tops (see fig. 5). The green and dry weight per plant, exclusive of roots, are given in Table 3.

TABLE 3. *Green and dry weight of wheat tops on unlimed soils*

| Soil | Green weight per plant, grams | Dry weight per plant, grams |
|---|---|---|
| Sand | .073 | .020 |
| Sand with humus | .174 | .048 |
| Humus | .343 | .0792 |

The wheat plants on the humus showed the effects of the low carbohydrate and high nitrogen content of the soil by forming several stems to the plant instead of a single stem as with those on the sand. This agrees with the results already obtained by several workers (7 and 8) on the influence of the carbon-nitrogen ratio.

## INFLUENCE OF ALKALINITY

*Heavy Application of Burnt Lime.*—The effect of alkalinity produced by the moderately heavy applications of air-slaked burnt lime was very unfavorable to all species except cedar. It is significant that cedar came up and looked thrifty on the limed mixture of sand and humus, whereas it died back on the unlimed, and that growth on the limed pure sand was practically the same as on unlimed sand instead of much inferior as it was with the other trees. On the limed humus it was prevented from coming up by the crust until a four days' rain from July 18 to 22 permitted the seeds to germinate on the surface, after which they grew well. Thus the alkalinity, though perhaps not favorable to the cedar, was far less unfavorable than to the other trees. The behavior of cedar corroborates Fernald's work on lithological factors (2), in which he brings out the preference of the species for limestone soils.

The unfavorable effect of alkalinity agrees with the work of Hoagland (5), who found that for barley alkalinity is more unfavorable than acidity for the same departure from the neutral point; here we see that alkalinity is harmful to trees as well as to barley. It is even probable that, except for certain trees like cedar, which grow best on lime soils, alkalinity is even more injurious to trees than to most crop plants.

The sugar maple seedlings, being transplanted only two days after the

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flats had been set out, received the effects of the higher alkalinities before there had been much decrease. On June 11, the day after transplanting, the sugar maples on the limed soils had dropped their leaves to a vertical position, one on the limed humus had already died, and but one plant had its leaves horizontal, and that was on limed sand. On the unlimed soils the leaves were horizontal except for a few which were at 45 degrees. By June 15 all the maples on the limed soils, except two on the sand, were dead, while all on the

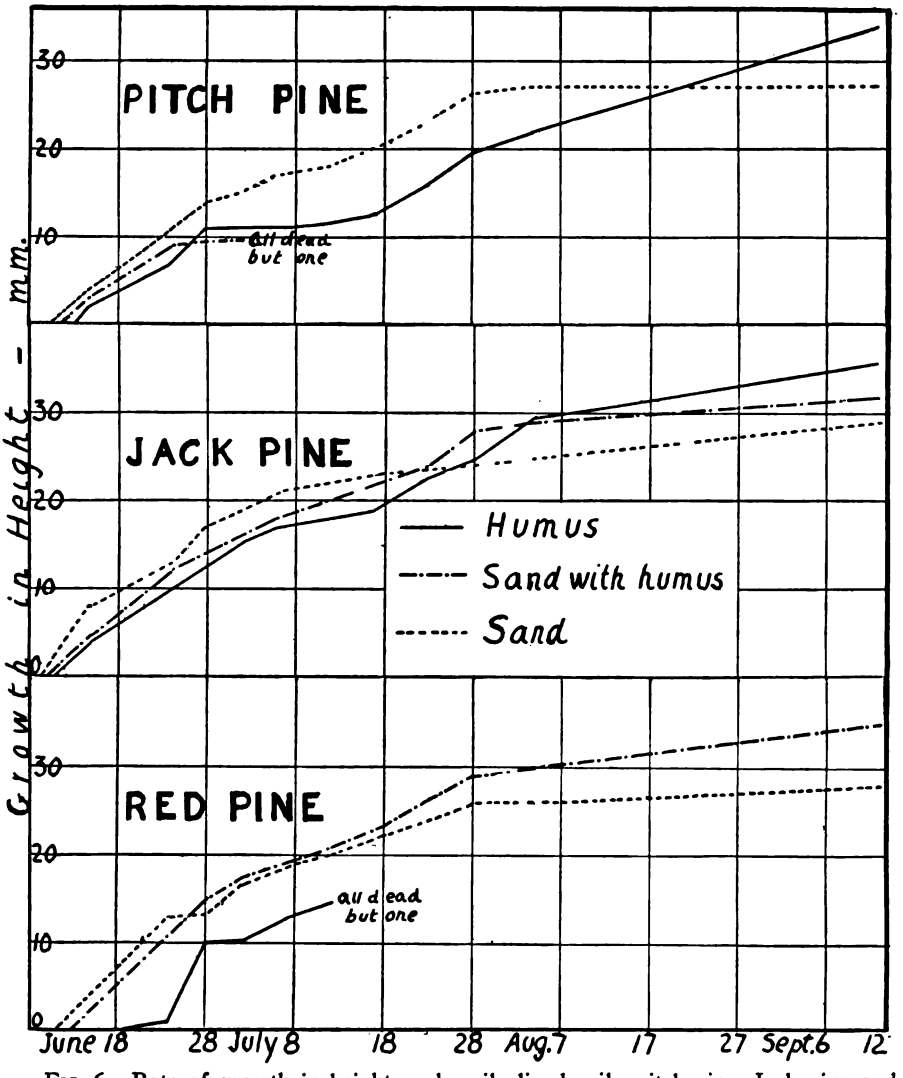


FIG. 6. Rate of growth in height on heavily lined soils, pitch pine, Jack pine and red pine seedlings. Shows the injurious effects of alkalinity, and its nullifying the benefits of the humus. Compare with figures 1 and 2 (remembering that figs. 1 and 2 are reduced about twice as much as fig. 6).

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unlimed soils were living and apparently thrifty. The two on the limed sand survived through the season, one with only one leaf, and made a small growth about equal to those on the unlimed sand. The limit of endurance of alkalinity by sugar maple is therefore probably less than .003 normal. The limits of acidity have not been determined, but it has been found growing in Maine in a humus with a hydrogen-ion concentration, determined by the Wherry method (11), of $P_H$ 4.5, or specific acidity of 300.

The toxicity of the burnt lime showed almost as soon as germination occurred. On the humus, probably on account of the surface crust, seedlings came up on only about a quarter of the rows, except pitch pine, which came up on about two thirds. On the sand and mixture of sand and humus germination was about the same as on the unlimed soils. But soon after germination a striking difference between limed and unlimed was apparent. By June 24 half of the Jack pine and a third of the pitch pine on the sand were unhealthy and shortly afterwards died; four fifths of the pitch pine and more than half of the Jack pine and red pine on the mixture of sand and humus were sickly and soon died. On the humus the Jack pine was in poor condition, the pitch pine had many unhealthy, and of the red pine only a small number were up.

From the point of view of survival the sand had the least ill effects of the three limed soils, and the mixture of sand and humus the most, though the humus was nearly as bad. By the middle of the season the flat containing limed sand and humus was almost bare, and the humus flat not much better. One red pine was living on the humus by July 12, and on the sand and humus all the pitch pine were dead by July 2. Records of the rate of growth on the limed soils are consequently based on a much smaller number of plants than those for unlimed soils.

Toxicity of burnt lime, though marked throughout the season, seems to have diminished somewhat in intensity by about July 17, or about 40 days after the exposure of the soil to the weather.

It is curious that the lime seemed to nullify to a considerable extent the beneficial influence of the humus. This may be due, in part at least, to the heavier application of lime received by the humus as compared with that given the other soils of the series.

The tops of a few individual plants showed the effect of the lime by becoming nearly white, not yellowish white. The stems, particularly on the sand and mixture of sand and humus, were short and crooked, and often the plants were lying prone against the soil, though alive and growing.

Root growth was very markedly affected by the lime. Back of the normal colored growing tip the root became brown and shriveled, sometimes for its entire length; often it would be unnaturally twisted, and in many cases the upper part came out of the ground and lay on the surface, the stem of the

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plant turning upward. The length of the roots on September 13 is given in Table 4.

TABLE 4. *Root growth on heavily limed soils*

| Species | Soil | | |
|---|---|---|---|
| | Average length of roots, cm. | | |
| | Sand | Sand with humus | Humus |
| Jack pine | 8 | 8 | 12.5 |
| Pitch pine | 7 | ... | 10 |
| Red pine | 9 | 7 | .... |
| White cedar | 5.4 | 2.5 | 5.2* |

* Younger than on other soils.

In one case the roots of 6 Jack pines growing on the limed sand had joined and, for a length of 4 millimeters from the end, were closely intertwined as though forming a single root-tip. The intertwined tips appeared healthy, the rest of the roots brown and shriveled, with perhaps 10 millimeters above ground. The seedlings were all living. Is this an example of mutual benefit through protection afforded by root excretions acting on the alkalinity of the soil?

At the end of the season the green weight of the plants was very much less on the limed than on the unlimed soils; the weight on the limed humus exceeded that on the limed sand by only a comparatively narrow margin. The weights per plant are given in Table 5.

TABLE 5. *Green weight per plant on heavily limed soils*

| Species | Soil | | |
|---|---|---|---|
| | Green weight per plant—grams | | |
| | Sand | Sand with humus | Humus |
| Jack pine | .129 | .132 | .158 |
| Pitch pine | .230 | .... | .252 |
| Red pine | .209 | .188 | .... |
| White cedar | .04 | .03 | .02* |

* Younger than on other soils.

Although all the trees except cedar suffered severely, the Jack pine seemed to suffer a little less than the others. A certain number of Jack pines pulled through on all soils, though only 6 survived on the humus.

Curiously enough, wheat on alkaline soils suffered very little as compared with trees. On the limed sand and mixture of sand and humus the height

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growth and weight were less than on the same soils without lime, but on humus there was very little difference between the limed and unlimed (see figure 5 and Tables 3 and 6). No matter how valuable experiments with herbs are in studying environmental relations of forest trees, toxicity and nutrition experiments in herbs must be applied to trees with caution. The green and dry weight per plant of the wheat, exclusive of roots, are given in Table 6.

TABLE 6. *Green and dry weight of wheat on heavily limed soils*

| Soil | Green weight per plant, grams | Dry weight per plant, grams |
|---|---|---|
| Sand | .028 | .008 |
| Sand with humus | .054 | .017 |
| Humus | .344 | .0786 |

*Light Application of Burnt Lime.*—It is not possible to give an absolute comparison of the influence of adding the small amount of burnt lime to the three soils studied, because the mild lime series was sown on June 23, 15 days after the others. Nevertheless some of the results are obviously due to differences in soil and are worth briefly considering.

The effect seems to have been intermediate between strong lime and absence of lime. On the coniferous trees, except cedar, the influence does not appear to have been beneficial, nor particularly injurious. Height growth throughout the season, always excepting cedar, was less than on the unlimed soils at the corresponding age, though this may be due partly to the late start as well as to the soil. Cedar found conditions more favorable on this series than on either of the others: in spite of the later start, height growth on both sand and on humus was nearly equal to that on unlimed soils by the end of the season (see fig. 2); there was also fair growth on the mixture of sand and humus, as compared with failure on this soil without lime.

Jack pine and pitch on the mixture of sand and humus passed the sand in height 3 to 5 days later than on unlimed soils. But red pine and cedar on the mixture did not catch up with that on the sand until the end of the season. By that time growth in height of all species on humus far surpassed that of the strongly limed humus, and, in spite of the later start, that on sand and on sand and humus equaled or surpassed that on the same soils with stronger lime.

Root growth was considerably less than on the unlimed series, probably partly on account of time of start and partly on account of soil, but showed greater length than on the more strongly limed series. Root area would undoubtedly have shown even greater superiority on the mild as against the strong lime.

In green weight there was not much difference between the lightly and heavily limed sandy soils, in spite of the late start of the former, but there

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was a noticeable difference in health and vigor. On humus the green weight of the lightly much surpassed that of the heavily limed plants; the smaller application of calcium did not mask the benefits of the humus. Table 7 gives the green weight per plant on the lightly limed soils.

TABLE 7. *Green weight on lightly limed soils*

| Species | Soil | | |
|---|---|---|---|
| | Green weight per plant—grams | | |
| | Sand | Sand with humus | Humus |
| Jack pine | .097 | .111 | .675 |
| Pitch pine | .184 | .206 | .807 |
| Red pine | .160 | .159 | .401 |
| White cedar | .023 | .015 | .040 |

The growth of wheat was remarkably stimulated by the small amount of lime added, and far surpassed that on the other soils both in height and in green weight (see fig. 6 on the extreme right). Table 8 gives the green and dry weight per plant of wheat, exclusive of roots, on this series.

TABLE 8. *Green and dry weight of wheat on lightly limed soils*

| Soil | Green weight per plant, grams | Dry weight per plant, grams |
|---|---|---|
| Sand | .060 | .017 |
| Sand with humus | .777 | .080 |
| Humus | 1.99 | .219 |

## Summary

The growth of certain coniferous trees, of a broadleaf tree, and of wheat, on soils of varying humus content, and on similar soils rendered alkaline by the addition of air-slaked burnt lime, was determined.

To eliminate the influence of humus on moisture-holding capacity, all soils were watered.

Growth in height, root growth, and green weight were very much greater on pure humus than on pure sand, and were intermediate on the mixture of sand with 4 percent humus by weight, though nearer that on the sand. Height growth on humus continued till the middle of September; on sand it fell off early in July, and on the mixture of sand and humus it diminished by the middle of July.

The favorable influence of humus is attributed to its nitrogen content. The value of humus as a nutrient and its influence on the rate of growth in certain forests, independently of its influence on moisture, appears to be amply demonstrated.

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Jack pine and pitch pine respond more to humus than do red pine or cedar. There is a possible indication that trees growing naturally on sterile soils are more strongly influenced by humus than those requiring better soils with other available nutrients than humus.

Cedar showed the beneficial effects of humus much less than the other species.

Wheat responded markedly to the humus, but less so than the coniferous trees except cedar. On the humus it showed the influence of the high nitrogen-low carbohydrate ratio.

Alkalinity produced by heavy applications of burnt lime was extremely unfavorable to all the trees except cedar. Sugar maple transplants died within 5 days, except for two on limed sand. A large proportion of the seedlings of the other species died, and those which survived made poor growth. Cedar came up on all three of the strongly limed soils, instead of on only the sand and humus as in the unlimed series, and grew slowly. The conifer roots on alkaline soils were brown and shriveled.

Alkalinity is more unfavorable to trees than acidity of the same departure from the neutral point. Cedar and other trees of lime soils may be an exception.

The toxicity of the burnt lime appeared to diminish somewhat after about 40 days' exposure, but still remained strong enough to be very unfavorable.

Wheat grew practically as well on the heavily limed as on the unlimed humus, showing the necessity for caution in applying to trees the results of nutrition studies in herbs.

In the lightly limed series growth in height, root growth, and green weight on the sand and mixture of sand and humus equaled or surpassed that on the stronger lime in spite of 15 days' later start. On the humus of this series all species excelled those on the more heavily limed humus in all respects and to a marked extent. Cedar did better on this series than on either of the others.

Wheat grew remarkably well on the light lime series, far surpassing that on the other soils.

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## ZOOLOGICAL ABSTRACTS

**Craighead, F. C.** Direct sunlight as a factor in forest insect control. *Proc. Ent. Soc. Washington,* **22**, 106–108. 1920.

Working with mesquite and ash logs he found that the subcortical temperature on the upper side of these logs exceeded the fatal temperature of insects working in the logs. The application of this principle in the control of insects working in logs is recommended. S. A. GRAHAM.

**Craighead, F. C., and Loughborough, W. K.** Temperatures fatal to larvae of the red-headed ash borer, as applicable to commercial kiln-drying. *Jour. Forestry,* **19**: 250–254. 1921.

In all tests above 128° F. with 100 percent relative humidity the borers were killed in from 1 to 2 hours. Four hours at 120° F. and 16 hours at 116° F. killed 50 percent of the larvae. Nineteen hours at 120° F. killed all the larvae. 100 percent mortality was secured in 45 hours at 116° F. and 70 hours at 110° F. Submergence in hot water gave the following results:

10 min. at 125° F. killed 50 percent; 1 hr., 75 percent.
30 min. at 120° F. killed 75 percent; 2½ hrs., 100 percent.

In dry air the experiments gave the following results:

10½ min. at 120° F. gave 100 percent dead.
5 min. at 122° F. gave 100 percent dead.
2 min. at 125° F. gave 100 percent dead.
2, 3, and 4 min. at 120° F. failed to kill.
16 min. at 118° did not kill nor did it cause cessation of activity.

In dry air all temperatures above 120° F. cause cessation of activity in two minutes. S. A. GRAHAM.

**Edmonson, Charles Howard.** Protozoa of the Devil's Lake complex, North Dakota. *Trans. Amer. Micro. Soc.,* 39, 167–198, pls. 18–19. 1920.

The salinity of the water of Devil's Lake amounts to approximately one percent at the present time, and is slowly increasing owing to the gradual recession of the lake by evaporation. This salinity seems to be responsible for a dearth of shell-bearing rhizopods and the absence of many common species of flagellates and ciliates. Otherwise the protozoan fauna of the lake is not unusual.

Experiments showed that the Protozoa inhabiting the lake can adjust themselves more readily to fresh water than the forms accustomed to fresh water can accommodate themselves to the saline water of the lake.

In all, 111 species were found in the lake: 13 species belonging to the Sarcodina, 22 species to the Mastigophora, and 76 species to the Infusoria. The proportion of species in the three groups corresponds favorably with that in a typical fresh-water lake.

One hundred and three species of algae have been found in Devil's Lake, of which five are typically marine forms. C. JUDAY.

**Hurd, W. E.** Influence of wind in the movement of insects. *U. S. Mon. Weather Rev.,* **48**, No. 2, 94–98. 1920.

A comprehensive review of the literature relating to the dissemination of adult and larval insects by wind. Twenty-three references are listed. S. A. GRAHAM.



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**Juday, Chancy.** The Cladocera of the Canadian Arctic Expedition, 1913–18. *Rept. Canadian Arctic Expedition, 1913–18,* Vol. VII, Part H, 1920.

The species of Cladocera listed in this report are from the shore of the Arctic Ocean (about 70° N. Lat.) in the general region of the mouth of the Mackenzie River. Entomostraca have frequently been collected from Greenland, Labrador, etc., on the east, and Alaska on the west, but the whole interior of Canada, from the southern boundary and northward, is almost an unknown region in regard to its entomostracan fauna. This report gives the first definite knowledge of the Arctic portion of this region.

Juday reports seven species of fresh-water and two of marine Cladocera. One of these, *Eurycerus glacialis,* is apparently confined to the Arctic regions; the others have wide distribution in all zones and are of no special significance here. G. S. Dodds.

**Marsh, C. Dwight.** The fresh-water Copepoda of the Canadian Arctic Expedition, 1913–18. *Rept. Canadian Arctic Expedition, 1913–18,* Vol. VII, Part J, 1920.

This report gives the first definite knowledge of the Copepoda of the Arctic portion of interior Canada. Thirteen species are listed. The list is of considerable interest, for while it contains certain cosmopolitan forms, as would be expected, it also includes others of special interest as part of Arctic faunas of other regions. G. S. Dodds.

**Saunders, Aretas A.** A distributional list of the birds of Montana, with notes on the migration and nesting of the better known species. *Cooper Orni. Club, Pacific Coast Avifauna,* No. 14. 194 pp., 35 figs., 1921.

Divides the State of Montana into six faunal regions: Southern Prairie, Northeastern Prairie, Northwestern Prairie, Southern Mountain, Northeastern Mountain, and Northwestern Mountain. In a preliminary classification of the bird associations the grass associations are divided into meadow, bench, and foothill; the water associations are divided into prairie lake, mountain lake, river, mountain stream, and cattail and tule marsh; the rock associations are not classified; the shrub associations are divided into willow thicket, sage-brush, wild-rose, and cinquefoil; the tree associations are divided into cottonwood grove, aspen grove, mixed broad-leaf and coniferous, yellow pine, lodgepole pine, white-bark pine, western white pine, Douglas fir, fir and tamarack, Englemann spruce, limber pine, and arbor-vitae; and the artificial associations are not classified. L. R. Dice.

**Stefansson, V.** Temperature factor in determining the age of maturity among the Eskimos. *Jour. Amer. Med. Assoc.,* 75, 669–70.

Eskimo girls of northern North America become mature at the early age of 10 to 13 years. These Eskimos, however, live during the winter in steamy houses kept constantly at a high temperature, and when they are outside they dress in very warm furs. They thus have a tropical or subtropical temperature in their personal environment, and their early maturity corresponds with that of races living in hot climates. On the contrary, the Dog Rib and Yellow Knife Indians of northern Canada do not mature earlier than north European whites, but the mode of life of these Indians is not well adapted to the climate, and they suffer much from the cold. L. R. Dice.

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# NOTES AND COMMENT

## A Reaction to a Variation in Light Intensity by the Coffee Leaf-Miner

While passing through a coffee grove near Lares, Porto Rico, on April 19, 1921, several small silver-white moths of the coffee leaf-miner, *Leucoptera coffeella* Stain. (Lepidoptera, Family Lyonetidae), were noted on the upper sides of the leaves. Cook & Horn, who had studied this insect in Cuba, state (p. 5, Bulletin No. 3, Estación Central Agronómica de Cuba): ". . . we have never seen an adult insect in the field, but have raised them in great abundance in our laboratory." On June 14, when passing through the same grove, not a moth was noted during a careful search, but looking beneath the leaves, several were soon found. The sun was shining brightly at the time; the April observations were made when the sky was overcast with clouds. Before departure from the grove the sun went under a cloud and a couple of moths were seen on the upper surface of the leaves. These observations on the reaction of the moth to sunlight and to clouds obscuring the sun have since been confirmed at several other widely separated localities. This is not a reaction to sunlight and shade, as coffee is practically always grown under the comparatively dense shade of other trees, but a reaction to the much reduced leaf-filtered sunlight and cloudiness.

The leaf-miner caterpillars, when fully grown, emerge from their mines and spin a cocoon on the underside of coffee leaves, or of the large leaves of other plants occurring in coffee groves. Under normal conditions, even in the most densely shaded groves, the cocoons *never* occur on the upper surface. A small coffee tree, the leaves of which happened to be infested with miners, was potted and placed in a corner on the covered gallery or porch of the Entomological Laboratory of the Experiment Station at Rio Piedras, P. R., where there was light, but never direct sunshine. A few days later eight cocoons of the leaf-miner were found on the upper surface of the leaves and none on the under surface. Other small coffee trees, transplanted at the same time to the yard of the laboratory where they were in the partial shade of some guava bushes, also had numerous freshly formed cocoons of *Leucoptera* on their leaves, but all on the underside. This shows that both the caterpillar and the moth of *Leucoptera coffeella* are remarkably sensitive to a variation in subdued light intensities.

George W. Wolcott

San Juan,
Porto Rico

## Notes on the Animal Habitats at Missoula, Montana

Missoula has an elevation of 3,223 feet, and is located in the broad valley at the junction of the Bitterroot River with the Clark Fork of the Columbia. On every side mountains rise several thousand feet above the valley. The summers and autumns are mild and pleasant; but the winters are severe, with many storms; and the springs are uncertain and backward.

Bunchgrass, which originally covered most of the floor of Bitterroot Valley, extends over the lower exposed slopes of the mountains. Along the streams is a fringe of deciduous trees and shrubs dominated by cottonwoods, but commonly containing such forms as western birch, alder, willows, yellow pine, dogwood, thorn, clematis, Symphoricarpos, elderberry, mountain maple, cherry, mountain ash, rose, and syringa. Some of these shrubs form thickets along the small streams in the mountain



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canyons. A few small meadows occur along the larger streams. Small areas on the exposed lower slopes of the mountains are covered by a scrubby growth, somewhat resembling chaparral, in which ninebark and service-berry are conspicuous species. In Lo-lo Canyon small patches of sagebrush were noted on the side exposed to the sun.

Yellow pine is the characteristic tree of the drier exposed mountain slopes which are not occupied by bunchgrass, the pine apparently not being able to withstand quite as much exposure to wind and sun as the grass. The slopes on which this tree is found are frequently very rocky. Yellow pine is found also in some of the drier places in the valley bottoms, and it seems frequently to succeed the cottonwoods in those parts of the valleys where the downcutting of the stream has lowered the water-level below the reach of the deciduous trees.

The moister, protected lower slopes of the mountains, and most of the higher slopes, are covered by a coniferous forest in which Douglas fir is the most characteristic tree, but which includes in places a goodly number of western larches. In some of the higher canyons lodgepole pine, Engelmann spruce, and grand fir were noted, but no trips to the higher parts of the mountains were made in this region, and no description can be given of the habitats of the higher altitudes.

The natural animal habitats of the region about Missoula may be tentatively listed as follows:

| | | |
|---|---|---|
| Aquatic | Canyon-thicket | Sagebrush |
| Shore | Douglas fir—larch | Bunchgrass |
| Meadow | Yellow-pine | Rocky-slope |
| Cottonwood | Scrub | Aerial |

Of modified habitats the Cultivated-field, Orchard, Burned-forest, and Edificarian are represented.

LEE R. DICE

## CONSERVATION WEEK IN NEW YORK

The first week in April is to be devoted by the New York City and State Federation of Womens' Clubs to arousing public interest in conservation. In addition to a pageant, one day is to be given to wild life, one to parks, and one day to forestry.

## SOCIETY AFFAIRS: THE VOLUNTARY CONTRIBUTIONS.

Each member of the Society received, with the announcement of the Toronto Meeting, a request for a voluntary contribution to be applied toward the removal of the deficit incurred in the publication of the first two volumes of ECOLOGY. The deficit at the end of the second volume is substantially less than at the end of the first, but ought, if possible, to be removed, preferably without raising the dues or drawing further on funds available for the other activities of the Society. It appeared at the time the request was sent that this deficit would be in the neighborhood of $500, toward which $200 was pledged by a person who prefers to remain unknown, on condition that the Society contribute an equal amount in addition to its regular dues. After the circulars had been mailed it was learned that the Brooklyn Botanic Garden is prepared to contribute for 1921, up to $300 as it had in 1920, thus reducing the needed sum to $200. At the Toronto meeting it was decided not to send out a supplementary circular. The conditional gift of $200 has been modified so that it will not be lost if the Society does not raise the full $200. Whatever the Society contributes up to this sum will be duplicated. Any amount received over and above the actual deficit will go towards an increase in the number of pages which is urgently needed to take care of the heavy demand for space.

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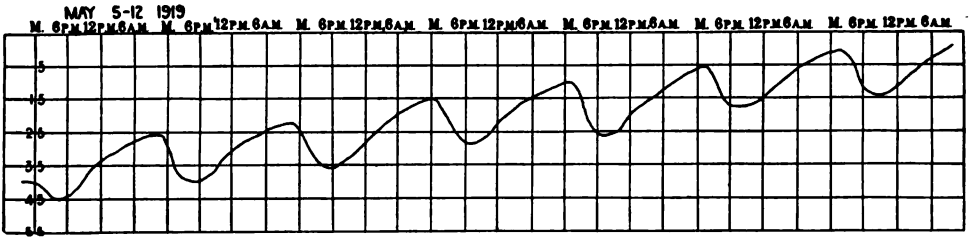


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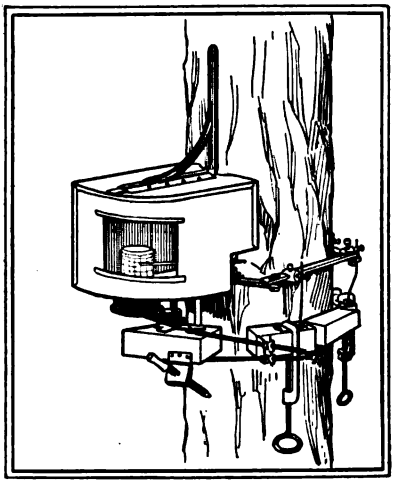

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# ECOLOGY

VOL. III APRIL, 1922 No. 2

## THE HUMANIZING OF ECOLOGY[1]

STEPHEN A. FORBES

*Chief Illinois State Natural History Survey*

It may seem to some of us questionable that ecology should need to be brought into any special or intimate relation to considerations of human welfare (which is what I mean by humanizing ecology)—questionable whether the so-called practical bias is not already too pronounced; whether, indeed, ecology as it should be pursued and developed by its specialists has, or ought to have, anything whatever to do, positively or negatively, with any other than those intellectual interests to which it appeals as a science; whether there is any more reason to discuss in an ecological society the economic bearings of ecology than those of astronomy or mathematics in their special society meetings. But, whatever may be our present attitude toward the general question, it has seemed to me that it might be helpful to us as ecologists to try to see what the humanistic relations of ecology actually are or might be made to become; after which we shall be in more favorable position to decide what, if anything, ought to be done about them. I think that we all well understand and appreciate the economic and other humanistic values and applications of botany, including bacteriology, of zoology, including entomology, of physiology, especially as related to the protection and restoration of health and hence to the prolongation of human life; and we can understand also how immensely each of these sciences has profited in its cultivation and development, in all its divisions and in all directions, because of these relations. Now, ecology as a separate subject cuts across the other biological sciences at right angles, forming an integral part of each and at the same time a bond of union between them.

Dealing with the relations of plants and animals, singly or associated, to their environments, organic as well as inorganic, ecology furnishes a line of contact of each of them with the interests and welfare of man; for he is a part, and in a multitude of cases an all-important part, of the environment of other forms of life. The relationship of man himself to his environment is

[1] Presidential address delivered before the Toronto meeting of Ecological Society of America, December 28, 1921.

[**Ecology,** Vol. III, No. 1 (pp. 1–88) was issued March 14, 1922]



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an inseparable part of ecology; for he also is an organism and other organisms are a part of *his* environment. Ecology, therefore, broadly conceived and rightly understood, instead of being an academic science merely, out of touch with humanistic interests, is really that part of every other biological science which brings it into immediate relation to human kind.

The applied—the applicable—part of each of these sciences is simply and solely the ecological element which enters into its make-up. If we take the ecology out of botany or zoology, or out of any of their principal subdivisions, we have nothing whatever of it left which is capable of application to the material welfare of man. Ecology is, in short, of all the biological sciences, the humanistic science *par excellence,* and if we deprive it of its economic factor we take the economics out of all biology. This is not only a demonstrable fact, it is a logical necessity. If ecology is the science of the relation of organisms to their environment, including, of course, the *interactions* between the environment and the organism, and if man himself is an organism, then the relations of interaction between plants and animals on the one hand, and man on the other, are parts of ecology, and they contain the whole of applied biology. I must dissent, therefore, from the statement that applied ecology is no part of ecology itself—from the idea that the interactions between beetles and wasps is a part of *their* ecology, but that the interactions between beetles and man, between wasps and man, is not ecology, but only something closely related to it. Such a statement can be justified only by setting man outside the general order of living nature in a class by himself, as fundamentally different from other living things as physiology is from chemistry, as engineering is from mathematics. We can do this, of course, if we choose, by an act of violence, but to do so is, in my judgment, injurious both to ecology in general and to the study of its humanistic applications. I would humanize ecology, therefore, first by taking the actions and relations of civilized man as fully into account in its definitions, divisions, and coordinations as those of any other kind of organism. The ecological system of the existing twentieth-century world must include the twentieth-century man as its dominant species—dominant, that is, in the sense of dynamic ecology as the most influential, the controlling member of his associate group. I would next seek to humanize it by urgently advising a careful study by economic biologists of the methods, contents, and products of general ecology, with a view to a knowledge of its bearings upon economic problems and its use in their solution; and by urging also an acquaintance by ecologists with the demands of applied biology sufficient to enable them to recognize and point out the bearings of the products of their own researches upon the problems of the economist. Not fusion, but intelligent cooperation, is what seems to me to be called for—a point which I may illustrate from my own observation and experience.

We have had in the service of the Natural History Survey of Illinois an

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ecologist and an entomologist engaged, among other things, upon the same economic problem—that of the life history of the codling-moth as affected by the varying meteorological conditions of successive years, and of different parts of the season in a single year. The economic object is to enable us to foretell in any year, by an observation of the weather of the advancing season, just when the orchardist may expect the beginning and culmination of that stage in the insect life history to which his insecticide must be applied. The entomologist has operated by the method of direct observation, with the aid of field laboratories equipped with apparatus for making continuous records of open-air temperatures, rainfall, humidity, and rate of evaporation; while the ecologist has used the experimental method in a laboratory provided with means of accurately *controlling* degrees of heat, light, moisture, air movement, and evaporation, thus studying separately the effect of various degrees and rates of change in each of the elements which enter into the complex of conditions that make up the weather of a day or a season—a complex which the *field entomologist* was compelled to take as a whole without distinction or separation of its parts. Now, it made no difference to the ecologist that his codling-moth was an economic insect; his studies were just as fruitful and their results as significant as if his choice had been made without reference to a possible economic application of his results. And it made no difference to the entomologist that the equipment and methods that he used had been devised for purposes much more general than those of economic entomology—perhaps with scarcely any idea of the possibility of their entomological application. But it was a decided advantage to both these investigators that they could keep continuous track of each other's work, checking each other's methods and comparing their conclusions as they went along. The entomologist completed his research and prepared his manuscript some months ago, but his paper has been held out of the press until lately in order that we might be quite sure of the essential harmony of the outcome of the two lines of work; and each has contributed to the common product important elements, scientific on the one hand and economic on the other, which could not possibly have been arrived at by either one alone.

In view of the widespread interest which ought, according to what I have been saying of the applicable values of ecology, to be taken in it by many classes of the people, I would further humanize ecology by eschewing its technical terms where they are not really necessary, except, of course, in papers intended solely for the technical ecologist. I am reminded here of the definition of ecology given, many years ago it is true, by a celebrated biologist, to the effect that it is the science which tells us what every one knows in language which no one can understand. It has got far beyond that point now in the novelty and originality of its disclosures, but it has made equal progress in the novelty and complexity of its terminology. This is useful, of course, to the specialist for its terseness and clearness, and so is unavoid-

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able. But I commend to those who would make the products of their work generally interesting and profitable the expedient of the author of a bulletin on the prairie vegetation of Illinois, who appended to his technical treatise a non-technical summary, to be read, I am sure, with pleasure and comprehension by any intelligent person, although one might search the latest and largest dictionaries in vain for the meaning of some of the terms of his main treatise.

Measures of this kind are particularly desirable if we are to take the next step in my humanization process—that of introducing courses in ecology into the curricula of all students preparing for the pursuit of any branch of economic biology as a vocation. To load it with technical terms, devised for the sake of completeness and not really necessary to its comprehension, is to make it difficult and repellent to those to whom it should be most attractive, and to whom it might become most useful. In time, of course, its necessary names and expressions will become familiar to all concerned, as has been the case in agronomy and economic entomology, but progress to this end will be hastened if the way of the student is paved with flagstones instead of boulders. And finally, I would seek to humanize ecology by drawing into the ecological fellowship every practitioner of applied biology, in whatever other division of science his principal interest may lie, for he is already an ecologist in act whether the fact be recognized by him or not; and to shut himself out from the broad general field of ecological intercourse and inquiry is to cut himself off from what should be, or might be made, the main sources of his scientific inspiration. This we can do by not only making him welcome to membership in the Ecological Society of America and by giving him a place on our programs, both of which we already do, but by filling in and smoothing over the line of cleavage which now separates at too many points the strict ecologist from the economist—ecology as a pure science, so-called, from the method and art of its application to the well-being of man. But in making our special plea for the more nearly complete humanization of ecology we must not lose sight of the fact that the essential, the indispensable function of ecology is the exploration and development of those parts of the general field which lie outside the range and beyond the reach of the student of applied biology as such; and in the organization and generalization of those products of the other biological sciences which, without its coordinating and unifying touch, are likely to remain as incoherent fragments of their separate sciences.

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# VARIATION IN FRESH-WATER MUSSELS

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## INTRODUCTION AND STATEMENT OF THE PROBLEM

Shells of fresh-water mussels are variable with respect to height, length, obesity, the relative proportions of these dimensions, strength of corrugations, intensity of rays, color of epidermis, of nacre, etc. Although various scattered observations in works devoted primarily to other investigations indicate that these variations are not fortuitous, yet it is only recently that any detailed and careful work has been done for the purpose of determining the relationship of such variations to the ecological conditions in which the shells are found.

A brief review of at least some of the observations on the variability of fresh-water mussel shells is necessary. The early systematists, particularly Lea, were inclined to disregard the fact of considerable intra-specific variability and to form a new species for every local variation. Later workers showed the identity of many of these early species, and consequently reduced their number considerably. However, it appears that all the work in this field has not yet been accomplished, and that many forms now described as distinct species are but variations connected with the environmental conditions.

Observations on the variations themselves and their probable dependence on the environment are not very numerous, however. Wetherby (1882) noted that some species vary more than others; and also that shells of mountainous regions are subject to the greatest variety of conditions, since the streams flow through more heterogeneous strata, contain a more variable amount of mineral matter, and, being subject to greater extremes in the rate of flow, transport more different kinds of sediment than is the case with lowland waters. Consequently, he believed that any inherent tendency to vary would be called out in this environment.



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Several European investigators have noted that the same species takes different forms in rapid and in quiet waters. Among these may be mentioned Israel (1910), who remarks on the extreme variability of *Unio crassus,* stating that it takes a special form in almost every brook. In slow-flowing brooks with mud bottoms this species is long, with gently curved lower margins, and has a thick crust of mud at the posterior end; in brooks with a strong current and a shale bottom without gravel the shells are shorter, resembling *U. litoralis,* having quite normal posterior markings, with no trace of any slimy encrustation. In the rapid streams the posterior ends of the shells may be stunted by the rather large boulders. He also states that in the same brook the mussels may differ according to the kind of bed and the force of the water; and that, generally speaking, in swift streams or small rapids the mussels are much shortened or truncated, often almost round or bluntly triangular. In streams that are slightly less rapid the shells are somewhat longer and seem to stand between those of swiftly flowing waters and those of quiet pools, even though one or both of the other conditions exist but a few feet away. The type-form is that of the quiet pools; the shape of the others seems to depend upon the movement of the boulders and the more or less firm bed. However, Israel points out that the glochidia of all the different forms, as well as the young shells, are alike, and hence concludes that he is dealing with only a single species.

Isely (1911 and 1913) observed that peculiarities of distribution are very probably to be traced back to the young shells, and that the conditions having most influence on them will be most potent in determining the character of the adults. He also found by experiment that the rate of growth of the shells is very variable for individuals of a single species in the same stream or in different streams, depending on season, food, oxygen supply, and various other conditions. Young mussels grow much more rapidly than older ones, and different species grow at different rates. The growth period is usually from April to September. It would seem, therefore, that environmental conditions, in order to be effective, would have to act on the young shells, and at the favorable period of the year.

Meek and Clark (1912), speaking of *Rotundaria tuberculata,* say that the shells become smaller and thinner downstream, and that the main difference between this species and *R. granifera* is to be found in the degree of inflation. Coker (1914) records a difference in commercial value between shells of the same species found in lakes and in river-lakes, a difference registered mainly in shape and thickness. Wilson and Clark (1914), in their study of the mussels of the Cumberland River and its tributaries, arrived at these conclusions: that of two closely related forms differing mainly in the degree of inflation and both found in the same river system, the flatter and less inflated forms are found in the tributaries and the upper part of the stream; and the more swollen shells are in the lower stretches of the river, where there

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is a weak current and considerable mud. Secondly, other characters besides inflation are dependent on the rate of stream flow, size of stream, and kind of bottom, so that characters used as specific distinctions at one point become valueless elsewhere. Again, faunas of widely separated tributaries are often quite similar. In other cases a certain species may demand special environmental conditions, and thus its distribution will depend on other factors than mere stream position. Finally, different streams show various degrees of difference between large and small-stream species. These investigators found that the mussels could be separated into four groups: (1) small-stream species, restricted to the upper portions of the river and to its tributaries; (2) large-stream species, restricted to the lower portions of the main river; (3) species universally distributed over the river; and (4) species restricted to a limited region. In particular, they observed the distribution of *Rotundaria tuberculata* and *R. granifera*. Since these forms have been treated at some length in this paper, the observations of Wilson and Clark regarding them will be referred to later. Danglade (1914) made somewhat similar observations in the Illinois River on this species and on *Amblema costata* and *Obliquaria reflexa*. He also observed that the shells tend to become smaller going downstream. While Utterback (1916) states that in the Osage River compressed forms are to be found in the headwaters where the water is shallower and swifter, and that these forms become more swollen and heavier farther downstream where the water is deeper and more sluggish. Adams, in his investigations of the fresh-water gastropod *Io* (1915), also observed changes in various shell-dimensions in relation to position on the stream. He found, in addition, that the size of the stream apparently influenced the size of the shell; in this case small shells were found in small streams and large shells in large streams.

The first work devoted solely to the study of the variations of the shells of fresh-water mussels appears to have been that of Grier (1920*a*). He compared certain shells of Lake Erie with corresponding species of the Upper Ohio, and found several apparent correlations between various morphological features and the environment. The Lake Erie shells tended to have broader growth-lines, brighter colors, and a more polished epidermis, and to be smaller and thinner. Specifically, he found that practically all the shells he examined were more inflated in Lake Erie, had a greater posterior development, a better developed posterior hinge-length, and less thick valves than the forms in the Ohio. The height of the shell appeared to vary independently of the environment. The size of the members of the groups, as a whole, apparently varied directly with the size of the stream. This does not agree with the results of Danglade (1914) and of Meek and Clark (1912), who found the larger shells in the smaller streams. Further studies were made by Grier on correlation of morphology and sex (1920*b*), of nacreous color and station (1920*c*), and

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of epidermal color and station (1920*d*). He found with regard to sex certain apparent correlations with morphological features; many of these results, however, can not be considered significant owing to the lack of a sufficient number of cases. Taking the five species in which more than fifteen shells were considered, he found that the female shells, on the whole, were more inflated and higher with a greater length of the anterior hinge-line. In *Fusconaia flava, Amblema plicata,* and *Lampsilis luteola,* the female also had a greater posterior development and a thicker shell, while the opposite held true for *Eurynia recta* and *Lampsilis ovata.* Grier's conclusions in his study of nacreous color were that the nacre tended to vary in color considerably more than is ordinarily recorded; that it tended to become lighter or more bluish going downstream, with the Lake Erie shells having a greater proportion of blues than those of the Upper Ohio or Maumee; that there was probably a peculiar kind of nacre for each drainage or for certain localities in a single drainage; and that nacreous color appeared to be correlated with sex, but not with age. Regarding epidermal colors, the same conclusions were found concerning large amount of variability, effect of the drainage basin and locality on epidermal color, and correlation with sex. There was no connection between age and color except that the older shells tended to become darker. The epidermis tended to darken going downstream and was darker in the Upper Ohio and Maumee than in Lake Erie. Rays were best developed in small streams, and disappeared with age.

As early as 1909 Ortmann had made similar observations regarding obesity and stream position. In his paper on the fresh-water mussels of the Tennessee drainage (1918), he noted that in certain shells a flat and compressed form was found in the headwaters, a swollen form in the large rivers, and an intermediate form in rivers of medium size. He used this difference in obesity as a distinguishing characteristic, putting the shells in certain varietal groups according as they measured more or less than a certain arbitrary figure. He carried this out for several species groups, finding in many cases that the form originally described and bearing the species name was really intermediate in so far as obesity was concerned. Later he made a special study (1920) of this apparent correlation of obesity and position on the stream in several species groups. Those which he found to be connected by intergrades he made one species with several varieties. In addition to confirming his former conclusions regarding decrease in obesity in the headwaters, he found that young shells on the average were more swollen than older ones; that less obese shells were frequently longer; and that a tuberculated form frequently lost its tubercles in the headwaters. On the other hand, he found many species that showed no trace of this greater obesity in larger streams, being approximately equally swollen along the whole river system. In a recent letter to Dr. Ortmann, Danglade confirms many of these conclusions. In particular, he finds that *Lampsilis anadontoides* and *L. fallaciosa* are not

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associated together to any noticeable extent, the former preferring the lower stretches of the large rivers and a shore bar of gravel or sand, while the latter seeks quiet waters and a soft or mud bottom near shore. He finds, differently from Grier, that those shells with clearer markings and more rays come from muddy streams where they are more or less hidden from the light. A great many other characters besides rapidity of flow and character of bottom affect the features of the shells, but, in general, swifter waters and harder bottoms mean more compressed shells, lighter epidermis, and lighter nacre. Danglade found this to hold true not only for the above-mentioned *anodontoides* and *fallaciosa,* but also for *Obliquaria reflexa, Obovaria olivaria, Megalonaias heros, Rotundaria tuberculata, Lampsilis ovata ventricosa,* and *Actinonaias carinata* (*ligamentina*).

In nearly all the above statements, the conclusions have been based on general observations rather than on accurate mathematical measurements. The only exceptions are the papers of Grier and of Ortmann (1920). Even here nothing beyond maxima, minima, and means of the shell dimensions have been considered. In one case the shells are grouped into those from Lake Erie and those from the Upper Ohio, and in the other computations are based on the shells taken from one locality regardless of the number of specimens. Nowhere has any treatment been made of the subject in which the environmental factors have been measured so that accurate mathematical proof of these above statements could be obtained, and actual correlation of shell variations and the environment be shown to exist.

The problem of this paper, then, really falls into two parts. First, to treat certain variations of the shells of fresh-water mussels in such a way that the dependence or lack of dependence of these variations on certain factors of their environment can be proved statistically. And, secondly, to show that several forms originally described as separate species are, in reality, only geographical or ecological races, differing from one another mainly in the degree of obesity, and abundantly connected by intergrades.

## Method

The material used was from the collection of the Carnegie Museum, Pittsburgh, Pa., Dr. W. J. Holland, director. The work was done under the guidance of Dr. A. E. Ortmann, who suggested the problem and the species to be used, and assisted in every possible way during the progress of the work. I wish to express my great appreciation to him for his aid in the preparation of this report. To Professor H. D. Fish, of the Department of Zoology of the University of Pittsburgh, I desire to make acknowledgment for his suggestions regarding the statistical treatment of the data. I wish also to express my gratitude for the aid that has come to me from other sources.

Approximately 1,150 shells were considered; these belong to the following species-groups:

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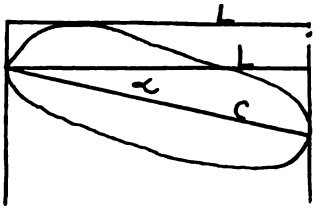
1. *Amblema peruviana.*
2. *Amblema perplicata.*
3. *Rotundaria tuberculata.*
4. *Ptychobranchus occidentale.*
5. *Ptychobranchus greenii.*
6. *Lampsilis orbiculata.*
7. *Truncilla torulosa.*
8. *Truncilla rangiana.*




Only those shells were considered the locality of which was known, a locality meaning—in practically every case—a definite point on a certain stream. The length and diameter of every shell were measured in tenths of a millimeter by means of a vernier caliper. The length was taken parallel to the hinge-line; the diameter was the greatest distance at right angles to this measured from left to right. The obesity was then found by dividing the diameter by the length and reducing to a percentage basis. In addition, the height, taken at right angles to the length, and measured dorso-ventrally, was taken for *Ptychobranchus occidentale* and *Lampsilis orbiculata.* The greatest length of the shell was also taken for the former species; and the distance from the dorsal margin to the point of greatest inflation for the latter. The reasons for taking these measurements will be brought out under the discussion of results. For all the *Truncillas,* the prominence of the tubercles was also estimated by means of an arbitrary grading scale. Wherever possible, the age and sex were noted for each shell; and, in certain species, the color of the nacre, of the epidermis, the relative smoothness, prominence of ridges, etc. The shells were then arranged and tabulated by localities, beginning downstream and going up each tributary as one arrived at it. In order to reduce the environmental factors to a statistical basis, it was decided to attempt to correlate these variations with stream-flow measurements. These measurements have been taken for several years by the United States Geological Survey and by various state commissions. Wherever possible, yearly averages were computed for all readings taken from 1899 to 1920 at all localities from the stream-flow of which might be obtained that of points where shells were available. The main source of information was the annual Water Supply Papers of the U. S. Geological Survey. These give measurements in

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cubic feet per second (second-feet), and are based on the size of the stream-bed and on the rate of flow. Maps were then made up, on which were indicated the points from which shells had been obtained, and the stations at which stream-flow measurements were available. By this means it was possible, in practically every case, to find a fairly accurate stream-flow measurement for a locality possessing shells. For several cases the stream-flow in five hundred second-feet was plotted on quadrille-ruled paper against the obesity in five tenths of a percent. These tables were then condensed, owing to the manner in which the shells were grouped, by setting up the following divisions based on size of stream-flow.

| | |
|---|---|
| 0–749 second-feet. | 8,250–25,249 second-feet. |
| 750–1,749 second-feet. | 25,250–40,249 second-feet. |
| 1,750–3,249 second-feet. | 40,250 and above second-feet. |
| 3,250–8,249 second-feet. | |

Against this was plotted the obesity in groups of two percent, or the arbitrary factor for tubercle development, etc. In this way each measurement was recorded separately (figures 1 and 4 illustrate this method of setting

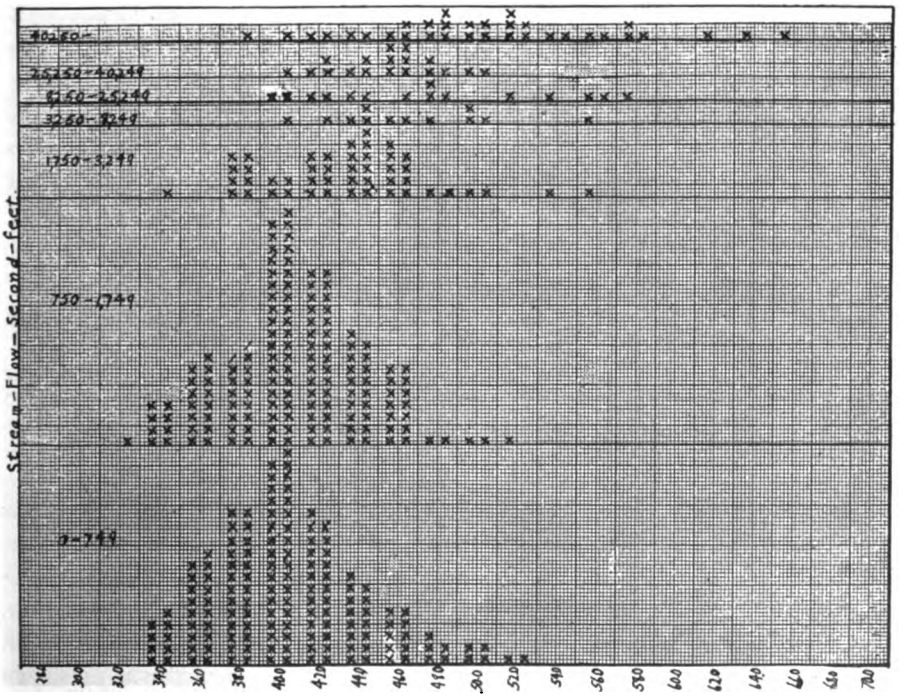


FIG. 1. Distribution of obesity in the *Amblema peruviana* group. Each shell is represented by an 'x'. The tendency for the shells to become more obese in the larger streams is clearly shown.

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down the results). In those species where the sex of a large number of shells was known, the shells were plotted in the usual manner and then plotted separately by sexes to discover any correlation based on sex differences (illustrated in figure 5). For the majority of these groups, the mean and the average deviation, as well as the probable error of both, were computed. The summary of these results is found in Tables I to IV. Curves were then drawn, based on these computations, for the mean and for the mean plus and minus the standard deviation. Smooth curves were then drawn on the same sheets to show the general trend of the variations regardless of fluctuations due to insufficient data (figure 2 is an example).

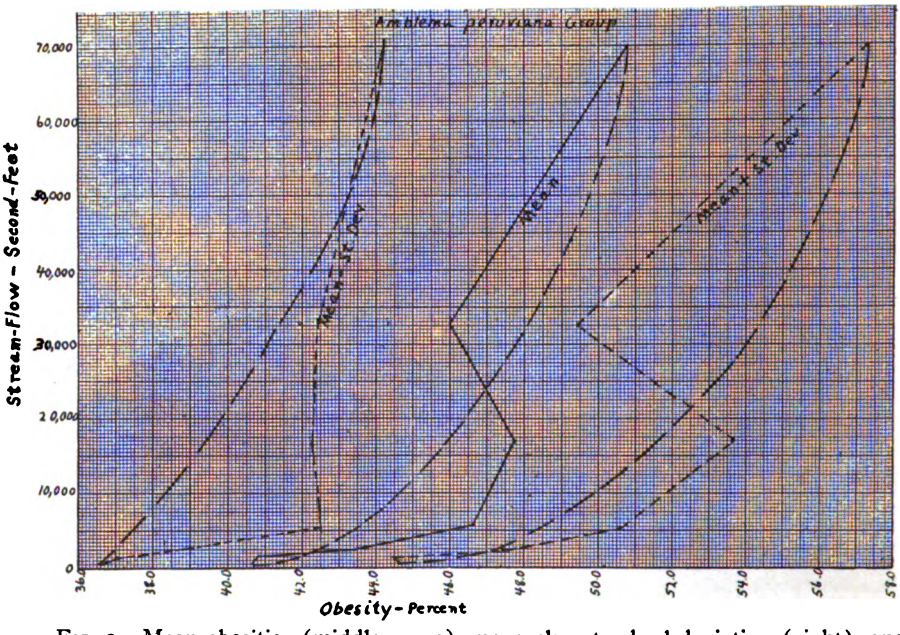


FIG. 2. Mean obesities (middle curve), mean plus standard deviation (right), and mean minus standard deviation (left), for all shells of the *Amblema peruviana* group, plotted for different sized streams. The data are the same as for figure 1, but are illustrated differently. The smoothed curves show the general tendency of the readings.

In order to determine whether or not the longer and hence the older shells were more swollen than the shorter or younger ones, approximately one hundred shells were taken in each species-group from a few localities, allowance being made for differences due to variations in amount of stream-flow. These shells were arranged according to length; and the obesity of the lower, middle, and upper thirds calculated with the standard deviations, as shown in Table II. Stepped curves for these means were then drawn (illustrated in figure 3).

The classification used was that of Ortmann (1912). Wherever closely

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TABLE I. *Size of shells in relation to size of streams in which the shells were found. Shell size expressed in obesity percent, stream size in second-feet of stream flow*

For each species the upper row of numbers represents mean obesity minus standard deviation; the middle row is mean obesity; the lowest row is mean obesity plus standard deviation.

| Species group | Stream flow in second-feet | | | | | | |
|---|---|---|---|---|---|---|---|
| | 0–749 | 750–1749 | 1750–3249 | 3250–8249 | 8250–25249 | 25250–40249 | 40250– |
| | *Obesity Percent* | | | | | | |
| *Amblema peruviana* | 36.627 | 37.182 | 39.112 | 42.477 | 42.004 | 42.446 | 44.198 |
| | 40.613 | 40.836 | 43.362 | 46.667 | 47.867 | 46.0 | 50.727 |
| | 44.599 | 44.490 | 47.612 | 50.857 | 53.730 | 49.554 | 57.256 |
| *Amblema perplicata* | 45.042 | 42.672 | 47.877 | 47.610 | 48.322 | | |
| | 48.133 | 48.435 | 51.889 | 50.0 | 53.149 | ..... | ..... |
| | 51.224 | 54.198 | 55.901 | 52.390 | 57.976 | | |
| *Rotundaria tuberculata* | 42.403 | 41.665 | 43.970 | 44.163 | 42.182 | 48.352 | 49.321 |
| | 49.714 | 46.714 | 49.440 | 49.0 | 47.714 | 51.333 | 55.2 |
| | 55.945 | 51.763 | 54.910 | 53.837 | 53.247 | 54.314 | 61.079 |
| *Ptychobranchus occidentale* | 25.557 | | 25.860 | 34.0 | | | |
| | 31.294 | | 32.782 | 35.0 | ..... | ..... | ..... |
| | 37.031 | | 39.704 | 36.0 | | | |
| *Ptychobranchus occidentale* ∝ | 1.786 | | 7.173 | 8.8 | | | |
| | 5.306 | | 11.766 | 9.9 | ..... | ..... | ..... |
| | 8.826 | | 16.359 | 11.0 | | | |
| *Ptychobranchus greenii* | 35.640 | 33.222 | ..... | 35.901 | 37.584 | | |
| | 37.6 | 36.182 | ..... | 38.5 | 40.7 | ..... | ..... |
| | 39.560 | 39.142 | ..... | 41.099 | 43.816 | | |
| *Lampsilis orbiculata* | | | 45.084 | ..... | 39.564 | 49.816 | 45.619 |
| | | | 51.0 | ..... | 47.334 | 54.640 | 50.667 |
| | | | 56.916 | ..... | 55.104 | 59.464 | 55.715 |
| *Lampsilis orbiculata* ♂ | | | 46.734 | ..... | 40.764 | 50.0 | 44.226 |
| | | | 50.0 | ..... | 43.0 | 51.0 | 48.462 |
| | | | 53.266 | ..... | 45.236 | 52.0 | 52.698 |
| *Lampsilis orbiculata* ♀ | | | 43.706 | ..... | 40.305 | 52.310 | 50.734 |
| | | | 51.5 | ..... | 50.0 | 56.286 | 54.0 |
| | | | 59.294 | ..... | 59.695 | 61.342 | 57.266 |
| *Truncilla torulosa* | 36.927 | 39.353 | 42.064 | 44.315 | 54.369 | 50.0 | 47.261 |
| | 39.556 | 41.0 | 45.8 | 47.440 | 54.667 | 50.0 | 50.133 |
| | 42.185 | 42.647 | 49.536 | 50.565 | 54.965 | 50.0 | 53.005 |
| *Truncilla torulosa* ♂ | 36.716 | 39.858 | 44.980 | 46.612 | 54.369 | 50.0 | 48.735 |
| | 39.5 | 41.250 | 47.667 | 48.667 | 54.667 | 50.0 | 50.0 |
| | 42.284 | 42.642 | 50.354 | 50.722 | 54.965 | 50.0 | 51.265 |
| *Truncilla torulosa* ♀ | 40.0 | 40.0 | 39.683 | 39.508 | ..... | ..... | 49.461 |
| | 40.0 | 41.0 | 43.0 | 46.308 | ..... | ..... | 52.4 |
| | 40.0 | 42.0 | 46.317 | 53.113 | ..... | ..... | 55.339 |
| *Truncilla torulosa. Tubercles* | 1.196 | .834 | 1.060 | 1.409 | 4.0 | 6.0 | 4.914 |
| | 1.667 | 1.286 | 1.7 | 2.120 | 4.0 | 6.0 | 5.533 |
| | 2.138 | 1.738 | 2.340 | 2.831 | 4.0 | 6.0 | 6.152 |
| *Truncilla rangiana* | 45.839 | 44.254 | 44.174 | ..... | 47.533 | | |
| | 48.667 | 47.838 | 46.476 | ..... | 49.889 | ..... | ..... |
| | 51.495 | 51.422 | 48.778 | ..... | 52.245 | | |
| *Truncilla rangiana* ♂ | 48.586 | 45.181 | 45.940 | ..... | 47.872 | | |
| | 50.0 | 47.905 | 47.739 | ..... | 50.154 | ..... | ..... |
| | 51.414 | 50.629 | 49.538 | ..... | 52.436 | | |
| *Truncilla rangiana* ♀ | 43.929 | 43.033 | 44.881 | ..... | 46.8 | ..... | ..... |
| | 47.5 | 47.333 | 46.861 | ..... | 49.2 | ..... | ..... |
| | 51.071 | 51.633 | 48.841 | ..... | 51.6 | ..... | ..... |
| *Truncilla rangiana. Tubercles* | 1.196 | 1.181 | 1.256 | ..... | 1.574 | | |
| | 1.667 | 1.703 | 1.881 | ..... | 1.889 | ..... | ..... |
| | 2.138 | 2.225 | 2.506 | ..... | 2.204 | | |

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related species were found to differ mainly in degree of obesity, due to differences in the size of streams, and intergrades were found in streams of intermediate size, these forms were considered as one species. However, when there was a sharp break in the degree of obesity, and this break was not connected with a difference in stream-flow; or when, for the same size streams, the obesity in one drainage was obviously different from that in another, specific names were retained. In order to avoid disputes regarding synonymy, shell measurements by various investigators were recorded and the obesity determined. Only those measurements were used which clearly had been obtained in a way similar to that used in this report. In those cases where the shells had been measured differently, as in Lea, and wherever else possible, the illustrations themselves were measured and the required percentages calculated. Lines of separation, based on degree of obesity, were more or less arbitrarily drawn, but no other procedure was possible in a series of intergrading forms.

TABLE II. *Relation of obesity percent to shell-length*

*For each species the upper row of numbers represents mean obesity minus standard deviation; the middle row is mean obesity; the lowest row is mean obesity plus standard deviation.*

| Species group | Shell length | | |
|---|---|---|---|
| | Shortest third | Middle third | Longest third |
| | *Obesity Percent* | | |
| *Amblema peruviana* | *38.756* | *45.230* | *37.058* |
| | 41.650 | 41.949 | 40.3 |
| | *44.544* | *38.668* | *43.542* |
| *Amblema perplicata* | *45.656* | *46.817* | *45.081* |
| | 53.438 | 52.848 | 49.875 |
| | *61.220* | *58.879* | *54.669* |
| *Rotundaria tuberculata* | *49.018* | *44.436* | *40.307* |
| | 56.4 | 50.412 | 44.571 |
| | *63.782* | *56.388* | *48.835* |
| *Ptychobranchus occidentale* | *25.527* | *27.864* | *25.581* |
| | 30.857 | 35.143 | 30.857 |
| | *36.187* | *42.422* | *36.133* |
| *Ptychobranchus greenii* | *37.548* | *36.462* | *35.895* |
| | 41.308 | 39.077 | 38.077 |
| | *45.068* | *41.692* | *40.259* |
| *Lampsilis orbiculata* | *43.2* | *48.255* | *47.671* |
| | 50.4 | 54.0 | 52.480 |
| | *57.6* | *59.745* | *57.289* |
| *Truncilla torulosa* | *40.216* | *44.5* | *41.102* |
| | 45.571 | 48.852 | 46.143 |
| | *50.926* | *53.204* | *51.184* |
| *Truncilla rangiana* | *44.761* | *41.691* | *44.208* |
| | 47.714 | 48.667 | 47.829 |
| | *50.667* | *55.643* | *51.450* |

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TABLE III. *Summary of shell measurements in relation to stream-flow, showing probable error, standard deviation, and probable error of standard deviation*

$M$ = Mean obesity, and probable error of mean. $s$ = Standard deviation and probable error of standard deviation.

| Species group | Stream-flow in second-feet | | | | | | |
|---|---|---|---|---|---|---|---|
| | 0–749 | 750–1749 | 1750–3249 | 3250–8249 | 8250–25249 | 25250–40249 | 40250—— |
| | *Obesity Percent* | | | | | | |
| *Amblema peruviana* | $M$ 40.613 ± .219 | 40.836 ± .204 | 43.362 ± .418 | 46.667 ± .815 | 47.867 ± 1.021 | 46.0 ± .550 | 50.727 ± .767 |
| | $s$ 3.986 ± .165 | 3.654 ± .144 | 4.250 ± .396 | 4.190 ± .577 | 5.863 ± .722 | 3.554 ± .411 | 6.529 ± .542 |
| *Amblema perplicata* | $M$ 48.133 ± .602 | 48.435 ± .573 | 51.889 ± .451 | 50.0 ± .609 | 53.149 ± .870 | | |
| | $s$ 3.091 ± .426 | 5.763 ± .405 | 4.012 ± .319 | 2.390 ± .431 | 4.827 ± .615 | | |
| *Rotundaria tuberculata* | $M$ 49.714 ± .996 | 46.714 ± .526 | 49.440 ± .738 | 49.0 ± .730 | 47.714 ± 1.410 | 51.333 ± .821 | 55.2 ± .627 |
| | $s$ 6.771 ± .705 | 5.049 ± .372 | 5.470 ± .522 | 4.837 ± .516 | 5.533 ± .997 | 2.981 ± .581 | 5.879 ± .443 |
| *Ptychobranchus occidentale* | $M$ 31.294 ± .939 | | 32.782 ± .973 | 35.0 ± .675 | | | |
| | $s$ 5.737 ± .664 | | 6.922 ± .688 | 1.0 ± .338 | | | |
| *Ptychobranchus occidentale* α | $M$ 5.306 ± .576 | | 11.766 ± .646 | 9.9 ± .525 | | | |
| | $s$ 3.520 ± .407 | | 4.593 ± .457 | 1.1 ± .371 | | | |
| *Ptychobranchus greenii* | $M$ 37.6 ± .591 | 36.182 ± .602 | ..... | 38.5 ± .438 | 40.7 ± .323 | | |
| | $s$ 1.960 ± .418 | 2.960 ± .424 | ..... | 2.599 ± .310 | 3.116 ± .235 | | |
| *Lampsilis orbiculata* | ..... | ..... | $M$ 51.0 ± 1.411 | ..... | 47.334 ± 1.747 | 54.640 ± .651 | 50.667 ± .655 |
| | ..... | ..... | $s$ 5.916 ± .997 | ..... | 7.770 ± 1.235 | 4.824 ± .460 | 5.048 ± .463 |
| *Lampsilis orbiculata* ♂ | ..... | ..... | $M$ 50.0 ± 1.272 | ..... | 43.0 ± .754 | 51.0 ± .675 | 48.462 ± .792 |
| | ..... | ..... | $s$ 3.266 ± .900 | ..... | 2.236 ± .533 | 1.0 ± .338 | 4.236 ± .560 |
| *Lampsilis orbiculata* ♀ | ..... | ..... | $M$ 51.5 ± 2.629 | ..... | 50.0 ± 3.270 | 56.286 ± .814 | 54.0 ± 1.886 |
| | ..... | ..... | $s$ 7.794 ± 1.859 | ..... | 9.695 ± 2.312 | 4.516 ± .576 | 3.266 ± .734 |
| *Truncilla torulosa* | $M$ 39.556 ± .591 | 41.0 ± .297 | 45.8 ± .797 | 47.440 ± .422 | 54.667 ± .116 | 50.0 ± 0 | 50.133 ± .242 |
| | $s$ 2.629 ± .417 | 1.647 ± .210 | 3.736 ± .563 | 3.125 ± .298 | ,298 ± .082 | 0 | 2.872 ± .171 |
| *Truncilla torulosa* ♂ | $M$ 39.5 ± .664 | 41.25 ± .332 | 47.667 ± .739 | 48.667 ± .401 | 54.667 ± .116 | 50.0 ± 0 | 50.0 ± .566 |
| | $s$ 2.784 ± .470 | 1.392 ± .235 | 2.687 ± .523 | 2.055 ± .283 | .298 ± .082 | 0 | 1.265 ± .270 |
| *Truncilla torulosa* ♀ | $M$ 40.0 ± 0 | 41.0 ± .675 | 43.0 ± 1.119 | 46.308 ± 1.273 | ..... | ..... | 52.4 ± .886 |
| | $s$ 0 | 1.0 ± .338 | 3.317 ± .791 | 6.805 ± .900 | ..... | ..... | 2.939 ± .627 |
| *Truncilla torulosa. Tubercles* | $M$ 1.667 ± .106 | 1.286 ± .081 | 1.7 ± .137 | 2.12 ± .096 | 4.0 ± 0 | 6.0 ± 0 | 5.533 ± .108 |
| | $s$ .471 ± .075 | .452 ± .058 | .640 ± .097 | .711 ± .068 | 0 | 0 | .619 ± .076 |
| *Truncilla rangiana* | $M$ 48.667 ± .636 | 47.838 ± .421 | 46.476 ± .240 | ..... | 49.889 ± .374 | | |
| | $s$ 2.828 ± .449 | 3.854 ± .297 | 2.302 ± .169 | ..... | 2.356 ± .265 | | |
| *Truncilla rangiana* ♂ | $M$ 50.0 ± .477 | 47.905 ± .4 | 47.739 ± .252 | ..... | 50.154 ± .427 | | |
| | $s$ 1.414 ± .337 | 2.724 ± .283 | 1.799 ± .179 | ..... | 2.282 ± .302 | | |
| *Truncilla rangiana* ♀ | $M$ 47.5 ± 1.205 | 47.333 ± .749 | 46.861 ± .306 | ..... | 49.2 ± .724 | | |
| | $s$ 3.571 ± .851 | 4.3 ± .529 | 1.98 ± .217 | ..... | 2.4 ± .512 | | |
| *Truncilla rangiana. Tubercles* | $M$ 1.667 ± .106 | 1.703 ± .059 | 1.881 ± .065 | ..... | 1.889 ± .050 | | |
| | $s$ .471 ± .075 | .522 ± .042 | .625 ± .046 | ..... | .315 ± .035 | | |

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## Results

Tables I and II summarize the mean obesities, and the means plus and minus the standard deviations, in relation to stream-flow and shell length.

Tables III and IV summarize the means and standard deviations, with the probable errors of each.

Table IV. *Relation of obesity percent to shell-length, showing probable error, standard deviation, and probable error of standard deviation*

$M$ = Mean obesity and probable error of mean.
$s$ = Standard deviation and probable error of standard deviation.

| Species group | | Shell length | | |
|---|---|---|---|---|
| | | Shortest third | Middle third | Longest third |
| | | *Obesity Percent* | | |
| *Amblema peruviana* | $M$ | 41.650±.309 | 41.949±.354 | 40.3 ±.346 |
| | $s$ | 2.894±.218 | 3.281±.251 | 3.242±.218 |
| *Amblema perplicata* | $M$ | 53.438±.928 | 52.848±.708 | 49.875±.572 |
| | $s$ | 7.782±.656 | 6.031±.501 | 4.794±.404 |
| *Rotundaria tuberculata* | $M$ | 56.4 ±.842 | 50.412±.691 | 44.571±.486 |
| | $s$ | 7.382±.595 | 5.976±.489 | 4.264±.344 |
| *Ptychobranchus occidentale* | $M$ | 30.857±.961 | 35.143±1.312 | 30.857±.951 |
| | $s$ | 5.330±.679 | 7.279±.928 | 5.276±.673 |
| *Ptychobranchus greenii* | $M$ | 41.308±.444 | 39.077±.346 | 38.077±.289 |
| | $s$ | 3.760±.314 | 2.615±.245 | 2.182±.204 |
| *Lampsilis orbiculata* | $M$ | 50.4 ±.971 | 54.0 ±.791 | 52.480±.649 |
| | $s$ | 7.2 ±.687 | 5.745±.559 | 4.809±.459 |
| *Truncilla torulosa* | $M$ | 45.571±.683 | 48.852±.565 | 46.143±.643 |
| | $s$ | 5.355±.483 | 4.352±.399 | 5.041±.454 |
| *Truncilla rangiana* | $M$ | 47.714±.337 | 48.667±.784 | 47.829±.413 |
| | $s$ | 2.953±.238 | 6.976±.554 | 3.621±.292 |

1. Group of *Amblema peruviana* (Lamarck). (437 shells.)

(*a*) **Amblema peruviana costata** (Rafinesque). Obesity 47 percent or less.

*Unio costatus* Conrad, 1836. Obesity 43.0.
*Quadrula undulata* Baker, 1898. Obesity 38.0; 38.4; 39.7; 40.0.
*Quadrula undulata* Simpson, 1914. Obesity 30.9; 36.4; 42.8.
*Quadrula costata* Vanatta, 1915. Obesity 36.4.

Here also belong two of the forms described by Simpson as *Quadrula plicata,* with obesity of 45.4 and 38.4.

(*b*) **Amblema peruviana** (Lamarck). Obesity over 47 percent.

*Quadrula plicata* Baker, 1898. Obesity 63.4; 65.0.
*Quadrula plicata* Simpson, 1914. Obesity 57.8.

Two other forms called *plicata* by Simpson belong under *costata.* However, the average of Simpson's three forms amounts to 47.2.

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Unfortunately, *A. peruviana* is the variety, and *costata* the original form, but priority in nomenclature compels use of this terminology. *Amblema peruviana* is the more swollen type of the larger rivers with smooth bottoms; there is a complete series of intergrades with the less obese *costata* of the smaller and more rapid streams with gravel or sandy bottoms. *Peruviana* is to be found in the Ohio and Mississippi drainages; it is mainly found in streams of considerable size and possesses high beaks and few undulations.

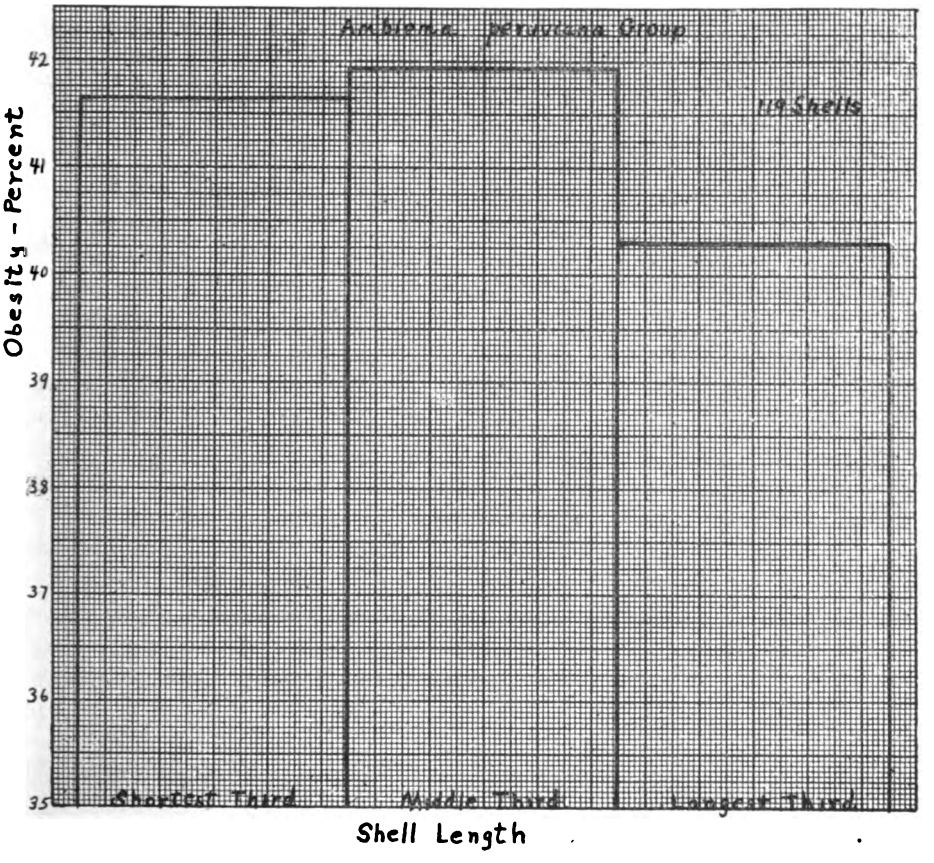


FIG. 3. Obesities of the longest, the middle, and the shortest thirds of 119 shells of the *Amblema peruviana* group. There is a tendency for the longest, hence the oldest, shells to be less obese.

Rafinesque's type form of *costata,* measured by Vanatta, is described as coming from a small creek in Kentucky. This variety is less swollen, has less prominent beaks, and is usually more undulated than *peruviana;* there are practically no other distinctions between the two forms. Conrad's point that *A. costata* has a more yellowish epidermis does not seem to hold when

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large numbers of shells are considered. Figure 1 and Tables I to IV show the dependence of the degree of obesity in this form upon the size of the stream-flow. It should be noted in this connection that four of the six *A. peruviana* found in streams of 1,750–3,250 second-feet come from the Ohio Canal at Columbus, Ohio. Here, although the stream-flow measured in second-feet is small, large-river conditions are present; for example, smooth, slowly flowing water and an even bed. It is just such an exception as this which goes far to prove the law that in this group of *Amblemas* smooth beds and slow, even-flowing streams result in more swollen forms than rugged beds and rapid waters. Furthermore, seven of the eleven *peruviana* from the smallest size streams come not from headwaters, but from small streams such as the Flint and Paint Rock Rivers and their tributaries not far from Florence, Alabama. These empty into the lower Tennessee at a point where the latter attains great size and possesses shells that are quite swollen. Although Isely has shown (1913) that mussels of this group are not given to excessive migration under favorable conditions, yet migration seems to be the most plausible explanation for the occurrence of these more swollen forms in streams of such small size. This distribution may be due to transportation of the glochidia by fish.

The fact that higher beaks and fewer undulations go with greater obesity are probably nothing more than growth phenomena. As the shell becomes more swollen the beaks will naturally become more prominent and be carried farther forwards, and it is quite likely that this would result also in a smoothing out of the wrinkles or undulations.

The material was deemed insufficient to attempt any correlation of sex and obesity since the sex of but a few of the shells was known. The changes occurring in the color of the nacre and of the epidermis in this species have been investigated by Grier (1920*c* and *d*). A curve for 119 shells shows that, to some degree at least, younger shells of this group are more swollen than older ones (figure 3).

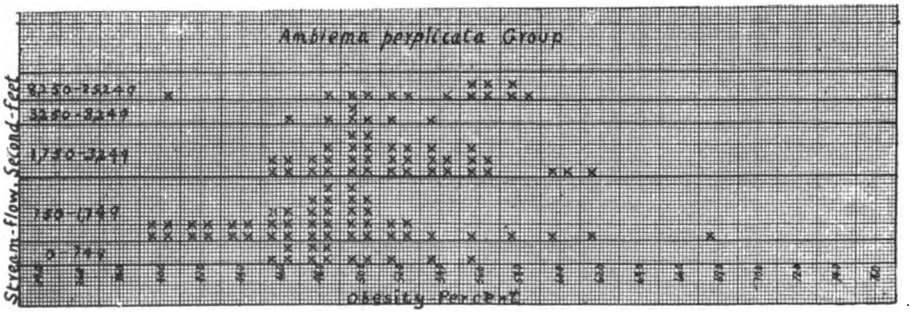


FIG. 4. Distribution of obesity in the *Amblema perplicata* group. A comparison of this figure with figure 1 shows the greater obesity of the *perplicata* as a whole, for the same size streams, as compared with the *peruviana* group.

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2. Group of *Amblema perplicata* (Conrad). (153 shells.)

(*a*) **Amblema perplicata elliottii** (Lea). Obesity 53 percent or less.

*Unio elliottii* Lea, 1858. Obesity 51.9.

*Quadrula elliottii* Simpson, 1914. Obesity 51.5.

One of the forms of *Quadrula perplicata* of Simpson belongs here. Obesity 41.4.

(*b*) **Amblema perplicata** (Conrad). Obesity more than 53 percent.

*Unio perplicatus* Conrad, 1850. Obesity —. (Original description, 1841.)

*Unio atro-costatus* Lea, 1848. Obesity 56.0.

*Unio brazosensis* Lea, 1869. Obesity 53.6.

*Unio lincecumii* Lea, 1869. Obesity 58.8.

*Unio pauciplicatus* Lea, 1874. Obesity 53.5.

*Quadrula perplicata* Simpson, 1914. Obesity 63.3.

The other form given by Simpson is *elliottii*.

The main difference between these two forms is the smaller degree of obesity for *elliottii*. Intergrading forms are quite common; the more swollen forms are found, as a general rule, in the larger streams; the more compressed *elliottii* in the headwaters. This group is confined mainly to streams flowing into the Gulf of Mexico, particularly in Alabama and Texas. This includes also the southern portion of the Mississippi and its tributaries, as well as a few more northern but western Mississippi tributaries, such as the Missouri River. Lea gives as his localities streams in Georgia, Alabama, Louisiana, and Texas.

Although the shells of the smaller streams are, as a whole, less swollen, yet there is a certain important exception which goes far to show the kind of conditions necessary to produce obesity-conditions, which it should be remembered are found in large streams. Twenty-one shells from the "Old River" of the Ouachita at Arkadelphia, Clark County, Arkansas, are not shown in figure 4 or in the curves. The "Old River" of the Ouachita is an ox-bow of the main stream and is entirely cut off from it at low water. Here lacustrine or large-stream conditions obtain, and we should expect from our knowledge of previous cases that more swollen forms would be found here. This is exactly the case; the shells from this part of the stream have a high degree of obesity, the mean of the group being 59.646, approximately 10 percent greater than the mean of the other shells in streams of similar size. For this reason it has been thought advisable to leave this set of shells out of the calculations. However, the occurrence of such a phenomenon only makes the case stronger. Furthermore, these twenty-one shells are as swollen as any large-stream *A. peruviana*.

In obesity, independent of size of stream, the group of *A. perplicata* is intermediate between *A. peruviana costata* and *A. peruviana*. The form

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called *elliottii* is closer to *costata; A. perplicata* is nearer *peruviana.* The reason why the *perplicata* group is not united with the *peruviana* group is that, when compared for streams of equal size, the former group is no longer intermediate. *A. perplicata elliottii* is more swollen than *A. peruviana costata,* but it is not found in larger streams; *A. perplicata* is nearly as swollen as *A. peruviana,* but it is found in very much smaller rivers. A comparison of figure 1 and figure 4, and of the means for the two species groups will show this fundamental difference. There is appended a list of the means of the two groups for the same size streams, which makes clear the greater obesity of *A. perplicata* as compared with the other group.

| *Stream-flow* | *A. peruviana* | *A. perplicata* |
|---|---|---|
| 0–749 | 40.613 | 48.133 |
| 750–1,749 | 40.836 | 48.435 |
| 1,750–3,249 | 43.362 | 51.889 |
| 3,250–8,249 | 46.667 | 50.0 |
| 8,250–25,249 | 47.867 | 53.149 |
| 25,250–40,249 | 46.0 | — — |
| 40,250——— | 50.727 | ——— |

What is the reason for this discrepancy? Why should shells of the Coosa River, for example, grow more swollen in tributaries of the same size than the shells of the Tennessee drainage, only a comparatively few miles away? Or why should shells of approximately the same geographical latitude be larger in streams flowing into the southern portions of the Mississippi than in streams tributary to the northern Mississippi? The distribution and the slight but distinct difference between these two species groups suggest a geographical separation in the past into two stocks of an originally homogeneous species. What basis is there for this conclusion when we consider the history of these streams?

The anomalous position of the shells of the Alabama drainage was pointed out by Wetherby (1882) and by Simpson (1900*a*), and the suggestion was made that the Tennessee and the Coosa were once connected. However, it seems probable that the separation took place fairly long ago, and that since Cretaceous times the Tennessee has flowed west at Chattanooga and not south. Ortmann (1912*b*) has shown that the streams west of the Alleghenies in the northeastern part of the country flowed north and northwest in Tertiary times. At this period there was no lower Mississippi River, the present Mississippi, Missouri, and Ohio Rivers being comparatively recent, due to the glacial invasion. He points out that the Allegheny Plateau is continued toward the southwest as the Cumberland Plateau; the latter, although interrupted by the present Mississippi Valley, appears to be connected with the old Ozarks, which extend to the Rockies. This was probably once a continuous elevation and formed the southern boundary of the interior basin.

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This basin, being also bounded on the east by the Allegheny Mountains and on the west by the Rockies, had an outlet only to the north. Ortmann believes that the present Tennessee and Cumberland Rivers were the headwaters of the northward-flowing streams of the Tertiary. The Glacial Period resulted in the changing of this drainage; the overflow of the resultant lakes being toward the south and southwest, the present system was formed nearly as constituted today. A study of the crayfishes (*Cambarus*) and of the fresh-water mussels was made by Ortmann, who found the following groups of fauna. The interior fauna is evidently the oldest; migrants from this region established themselves on the Atlantic Coast. One group migrated across the Alleghenian Divide; another group evidently went along the Erigan River, one of the northern outlets, but did not reach farther south than the Carolinas; while still another group probably arose on the southern Atlantic slope, or on the Gulf Plain, and migrated north along the Atlantic Coast or was confined to the southern portion of the Mississippi Valley. And, finally, there was the St. Lawrence fauna.

This brief account of the geologic history of the interior basin is offered in partial explanation of the distribution of *A. perplicata* and of *A. peruviana*. These two forms are different, very probably because they were inhabitants of quite distinct drainage systems as far back as the Tertiary. A divide separated the interior-basin streams from those flowing into the Gulf; and the Ozarks were a barrier between the Red River and the streams farther north. The occasional occurrence of *perplicata* west of the Mississippi, in the Missouri basin, may be explained by the fact that the Mississippi itself, as well as the Missouri, are effective barriers against the migration of mussels.

It has been suggested that the resemblance between the fauna of the Tennessee and of the Coosa is due to an original connection between the two streams. However, this slight resemblance does not necessarily prove a common drainage basin. Such distributional phenomena might be due to quite recent stream-capture, the tributaries of the Coosa encroaching upon those of the Tennessee, or they might be the result of transportation by various agencies. It is enough to show that these drainage basins were at one time distinct to offer a possible explanation of the differences in their fauna.

The measurements of 97 shells show that for this group also the younger shells are more swollen than the older ones.

3. Group of *Rotundaria tuberculata* (Rafinesque). (169 shells.)
   (*a*) **Rotundaria tuberculata** (Rafinesque). Obesity 57 percent or less.
      *Unio tuberculatus* Conrad, 1836. Obesity 53.5.
      *Quadrula verrucosa* Baker, 1898. Obesity 42.2♀; 41.8♂.
      *Quadrula tuberculata* Simpson, 1914. Obesity 36.8; 44.0; 46.7.
      *Quadrula tuberculata* Vanatta, 1915. Obesity 49.2.
   (*b*) **Rotundaria tuberculata granifera** (Lea). Obesity more than 57 percent.

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*Unio granifera* Lea, 1838. Obesity 72.1.
*Quadrula granifera* Simpson, 1914. Obesity 58.4; 71.7.

The differences between these two forms are in degree of obesity and number and prominence of tubercles. *Granifera* is more swollen and more tuberculated than *tuberculata,* and is frequently smaller. The reduction in size appears to bear out the statement of Ortmann (1920) that more swollen shells make up for their greater obesity by being shorter than the flatter shells. The distinction based upon strength of tubercles is not clear-cut and does not seem to be closely correlated with obesity. Simpson and Lea disagree about the relative prominence of the tubercles; the former says that those of *granifera* are stronger, the latter that they are smaller. Lea's specimen of *granifera* came from the Ohio River near Cincinnati; and Rafinesque's *tuberculata* from the Ohio River, no definite locality being given. Conrad states that this species is not found in Alabama south of the Tennessee River and its tributaries—another instance of the peculiarity of the fauna of the Coosa, Cahaba, etc.

Wilson and Clark (1914) have already suggested that *tuberculata* and *granifera* are connected by intergrades, the obesity depending on the size of the stream. The present investigation shows this to be the case, the larger *granifera* being practically confined to the larger streams. All cases of its occurrence in streams of less than 1,750 second-feet are in those rivers that are tributary to the Tennessee near Florence, Alabama, and can be explained as the result of migration from the broader and deeper Tennessee. A similar case was pointed out in discussing the *Amblema peruviana* group.

To a very decided degree young shells of this group are more swollen than older ones.

4. Group of *Ptychobranchus occidentale* (Conrad). (42 shells.)

Lack of a sufficient number of shells makes it impossible to state definitely the facts in this case. However, based on the material at hand, the following purely tentative suggestions are made.

If obesity is used as a basis of classification, the following groups can be set up:

(*a*) **Ptychobranchus occidentale clintonense** (Simpson). Obesity 32 percent or less.
*Ptychobranchus clintonensis* Simpson, 1900. Obesity 30.1.
*Ptychobranchus clintonense* Simpson, 1914. Obesity 31.1.

(*b*) **Ptychobranchus occidentale** (Conrad). Obesity over 32 percent.
*Unio occidentalis* Conrad, 1836. Obesity 32.7.
*Lampsilis occidentalis* Simpson, 1914. Obesity 37.5♀; 39.9♀.

However, these two forms do not differ only in obesity; the more swollen form has the beak pushed far forward, producing a "hump." The flatter forms are not humped. The amount of displacement of the beak can be

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measured in degrees and recorded. This group might then be divided into those forms having a hump of 10 degrees or less, and those with a hump of over 10 degrees. However, a measurement of Conrad's figure for *Unio occidentalis* shows no displacement or a value of 0 degrees. On the basis of this, we should be forced to make *occidentale* the flat form, of which *clintonense* is just a synonymous term. Although the amount of displacement of Simpson's *clintonense* is unknown, the slight obesity very probably means a small or no hump. Another name would then have to be applied to the more humped and swollen form. We would then have as an alternative to the above:

(*a*) **Ptychobranchus occidentale** (Conrad). Displacement of beak 10 degrees or less.
*Unio occidentalis* Conrad, 1836. Displacement 0 degrees.
*Ptychobranchus clintonensis* Simpson, 1900.
*Ptychobranchus clintonense* Simpson, 1914.

(*b*) Dr. Ortmann has suggested the name of **Ptychobranchus camelloides.** Displacement of beak over 10 degrees.
*Lampsilis occidentalis* Simpson, 1914.

It is probable that the latter is the correct arrangement, *occidentale* being that form with a beak displacement of 10 degrees or less, or else that form with an obesity of 33 percent or less. This would include Conrad's *occidentalis* on either basis. Another difference between the two forms, though not without considerable exception, is that the more swollen form has, in general, clearer and stronger rays on the shell. Both Simpson's more swollen and flatter shells come from the Little Red River, Arkansas; and Conrad's specimen comes from the Currant River in the same state. The species appears to grow flatter in the White River and its tributaries than in the Red or the Arkansas River and their tributaries; the latter streams, however, are larger.

In so far as the material permits, we may say of this group that the more swollen forms with a more pronounced hump are to be found in the larger streams, and that the flatter forms with practically no hump are confined to the smaller rivers. Of course, it may be that the reason why the flatter forms are less humped is the method of measurement. Since the length is measured parallel to the hinge-line, a greater displacement of the beak would mean a shorter length and hence greater obesity. However, this does not affect the fundamental principle involved, which will hold whether obesity or amount of displacement of the beak be the character chosen.

The method of determining the amount of displacement was as follows. If a shell be measured parallel to the hinge-line ($L$), and then the total length of the shell be taken ($C$), the cosine of the angle $\alpha$ can be easily found by dividing $L$ by $C$. This angle gives the amount of displacement of the beak,

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for as the beak is placed further forwards, $L$ becomes less and $\alpha$ increases. If $L$ and $C$ correspond, then $\alpha$ is equal to 0 degrees. The following diagram will explain the method of measurement.

Measurement of all the shells of this group (42) fails to show any relation between obesity and age. This may be due to an insufficient amount of material.

5. Group of *Ptychobranchus greenii* (Conrad). (78 shells.)

(*a*) **Ptychobranchus greenii flavescens** (Lea). Obesity 38.5 percent or less.

*Unio flavescens* Lea, 1848. Obesity 38.4.

Here also belong one of the specimens measured by Simpson (1914) as *Ptychobranchus greeni,* obesity 34.9, and two of the specimens which he considers under *Ptychobranchus foremianium,* obesity 35.1 and 37.1.

(*b*) **Ptychobranchus greenii** (Conrad). Obesity more than 38.5 percent, but less than 41.3 percent.

*Unio greenii* Conrad, 1836. Obesity 41.1.

*Unio velatus* Conrad, 1854. Obesity 39.6.

One of the *Ptychobranchus greeni* of Simpson. Obesity 40.8.

(*c*) **Ptychobranchus greenii foremianium** (Lea). Obesity 41.3 percent or more.

*Unio foremianius* Lea, 1842. Obesity 41.8.

*Unio simplex* Lea, 1848. Obesity 45.1.

*Unio woodwardianus* Lea, 1859. Obesity 46.5.

*Ptychobranchus foremianium* Simpson, 1914. Obesity 45.7; 49.1; the other two specimens are *flavescens.*

Two of the specimens of *Ptychobranchus greeni* Simpson, 1914. Obesity 45.0 and 50.0.

The reason for forming three divisions of this group is that the specific name was originally applied to the intermediate form. In addition to the difference in obesity, it may be said that, generally speaking, the more swollen form—*i.e., foremianium*—is more triangular in shape, and possesses a lighter epidermis, more marked by blotches than is true of the flatter form. But there are many exceptions to this statement; many of the *foremianium* type, for example, being practically free from any markings. There is also probably a difference in distribution of these races. *Flavescens* is found mainly in the Cahaba, Black Warrior, and Tallapoosa Rivers, although occasionally appearing in the Coosa. Lea's specimen comes from the Black Warrior River. *Greenii* is to be found in all these streams; Conrad's *greenii* comes from the Black Warrior, his *velatus* from the St. Fois River. *Foremianium* is practically confined to the Coosa and its tributaries, though occasionally occurring in other streams. Lea says that his *simplex* comes from the Black

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Warrior River; however, the measurement of obesity, 45.1, is much greater than that of any of the dozen specimens of the Black Warrior which are in the Museum collection; shells of this size occur in these specimens only in the lower Coosa. Lea's *foremianius* comes from the Coosa River, and his *woodwardianus* from the headwaters of the Coosa, and from the Etowah and Conasauga Rivers.

Examination of Tables I to IV will show clearly the greater obesity which shells of this species attain in the larger rivers. Furthermore, the younger shells tend to be more swollen than the older ones.

6. Group of *Lampsilis orbiculata* (Hildreth). (74 shells.)

(*a*) **Lampsilis orbiculata** (Hildreth). Obesity 55 percent or less.

*Unio orbiculatus* Hildreth, 1828. Obesity 70.0 (?).

*Unio crassus* Conrad, 1836. Obesity 48.3 ♂.

*Lampsilis orbiculata* Simpson, 1914. Obesity 40.0 ♂; 47.7 ♀.

*Lampsilis higginsi* var. *grandis* Simpson, 1914. Obesity 42.8 ♂; 52.7 ♀.

(*b*) **Lampsilis orbiculata higginsii** (Lea). Obesity more than 55 percent.

*Unio higginsii* Lea, 1862. Obesity 59.0 ♂.

*Lampsilis higginsi* Simpson, 1914. Obesity 56.0 ♂; 57.1 ♀.

Hildreth's measurement of 70 percent for the obesity of his specimen is evidently an error. None of the seventy-four shells measured for this group exceed 66 percent; and Dr. Ortmann states that he has never seen a shell of this group as swollen as that given by Hildreth. For these reasons Hildreth's figure has been disregarded in the above classification. If his measurement were correct, it would necessitate the formation of probably three varieties, with *orbiculata* as the most swollen. This is directly contrary to the accepted nomenclature of a flat *orbiculata* and a more swollen *higginsii*.

There seems to be a slight tendency for the more swollen forms to have a lighter epidermis. The localities given for *orbiculata* are Ohio, Indiana, and Illinois, usually not farther south; and for *higginsii*, Muscatine, Iowa. Hildreth's specimens come from the Muskingum River.

In *Lampsilis* the distinction between the sexes is quite easily seen in the shells of most specimens; this gives an opportunity to determine if there is any correlation between sex and obesity. Allowing for the small number of specimens, there appears to be a positive correlation in this species between highly obese and female shells. This result was obtained by considering the sexes separately, after having grouped them without such distinction. The means are as follows:

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| Stream-flow | All shells | Male shells | Female shells |
|---|---|---|---|
| 0–3,249 | 51.0 | 50.0 | 51.5 |
| 3,250–8,249 | ..... | ..... | ..... |
| 8,250–25,249 | 47.334 | 43.0 | 50.0 |
| 25,250–40,249 | 54.640 | 51.0 | 56.286 |
| 40,250 and over | 50.667 | 48.462 | 54.0 |

In every case the female shells have a higher average obesity than do the shells of both sexes taken together.

Although the degree of obesity seems to form a continuous series, yet it can not be said that obesity is, to any great extent, dependent upon the size of the stream (Table I). Whatever correlation there is between obesity and age shows that the younger shells are less swollen (Table II), a phenomenon which is just the opposite to most of the cases heretofore considered.

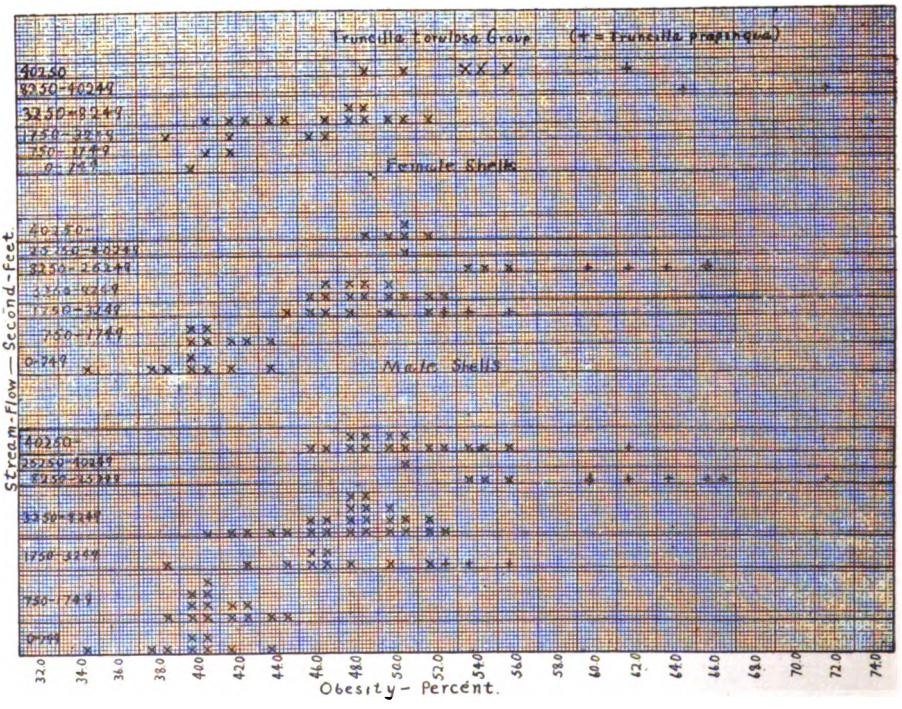


FIG. 5. Distribution of obesity in the *Truncilla torulosa* group. At the bottom is shown the distribution for the group as a whole, and above for each of the two sexes separately. The greater obesity of the male shells can be seen, as well as the lack of intergrading forms between *T. propinqua* (represented by +) and the rest of the group.

7. Group of *Truncilla torulosa* (Rafinesque). (93 shells.)

(*a*) **Truncilla torulosa gubernaculum** (Reeve). Obesity 49 percent or less; tubercles poorly developed.

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*Unio gubernaculum* Reeve, 1868. Reeve pictures a female shell, but gives no dorsal view; hence we can not know the obesity of his specimen.

*Truncilla perplexa* Simpson, 1914. This includes the flatter of his three specimens. Obesity 44.8♂; 41.4♀. However, we know nothing about the development of the tubercles on these shells.

(*b*) **Truncilla torulosa** (Rafinesque). Obesity more than 49 percent; tubercles well developed.

*Unio perplexus* Lea, 1831. Obesity 57.0♂.

*Unio gibbosus* Conrad, 1836. Obesity 55.9♂.

*Truncilla perplexa* Simpson, 1914. Obesity 56.0♂. The other two specimens are *gubernaculum*.

*Truncilla torulosa* Vanatta, 1915. Obesity 51.5; 55.3; 62.5.

The first two of these are the *torulosa* of Rafinesque; the last is Rafinesque's *gibbosa*.

(*c*) **Truncilla propinqua** (Lea). Obesity more than 52.5 percent. Tubercles intermediate in development between those of *torulosa* and *gubernaculum*.

*Unio propinquus* Lea, 1862. Obesity 61.3♂.

*Truncilla propinqua* Simpson, 1914. Obesity 60.0♂; 62.2♂; 55.2♀; 57.8♀.

*Truncilla propinqua* does not intergrade with the other two forms, in so far as obesity is concerned. Hence it is considered as a separate species. For any given size of stream, the most swollen shells are apt to be *propinqua;* and there is a definite break between them and the less obese forms, which seem to constitute a more or less intergrading series of their own. *Propinqua* shells have not entered into the calculations or the curves and are distinctly marked in figure 5.

Lea's specimen of *propinquus* came from the vicinity of Tuscumbia, Alabama; the forms considered in the present report come from the vicinity around the lower Clinch. Conrad gives as the habitat of *torulosa* the Wabash (?), the Scioto (?), and the Tennessee as far south as Florence, Alabama. The specimens measured in this report have all come from the lower Tennessee; the *gubernaculum* shells are from the tributaries of the upper Tennessee.

The relation between degree of obesity and size of stream is clearly seen (figure 5). The flatter forms of this group are to be found in the smaller streams; the more swollen shells in the larger streams. In this group the male shells seem to be more swollen. The following is a table of means:

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| Stream-flow | All shells | Male shells | Female shells |
|---|---|---|---|
| 0–749 | 39.556 | 39.5 | 40.0 |
| 750–1,749 | 41.0 | 41.25 | 41.0 |
| 1,750–3,249 | 45.8 | 47.667 | 43.0 |
| 3,250–8,249 | 47.44 | 48.667 | 46.308 |
| 8,250–25,249 | 54.667 | 54.667 | ..... |
| 25,250–40,249 | 50.0 (1 shell) | 50.0 | ..... |
| 40,250 | 50.133 | 50.0 | 52.4 |

This is just the opposite of what was found in *Lampsilis orbiculata,* where the female shells were more swollen.

With this group the prominence of the tubercles was also measured by giving arbitrary numbers to the various shells, based on tubercle development. Those shells having no or very slight tubercles were placed in class 1; those with the strongest tubercles in class 6. Figure 6 shows that the larger

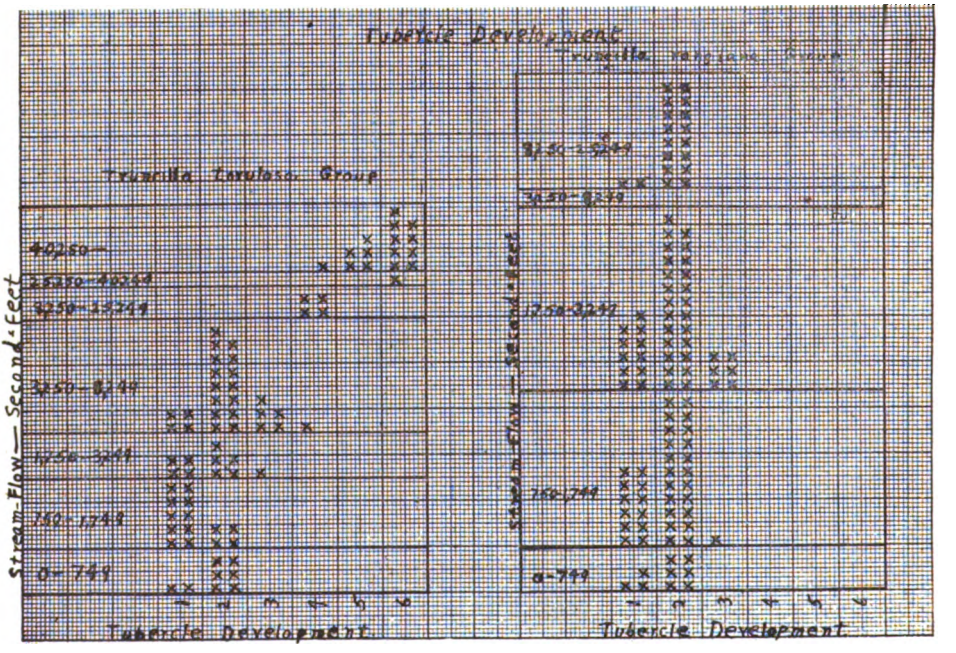


FIG. 6. Distribution of tubercle development in the two *Truncilla* groups. The numbers on the base-line represent degrees of tubercle development: a shell graded 1 has no or practically no tubercles; a shell graded 6 is strongly tuberculated. The correlation between strong tubercle development and large stream-flow on the one hand, and between lack of tubercles and small stream-flow on the other hand, is clearly seen.

streams have shells with the strongest tubercles, considering *torulosa* and *gubernaculum*. *Propinqua* specimens are more or less intermediate in

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strength of tubercles and position on the stream, even though they are not intermediate when grouped for obesity.

For this group there is apparently little correlation between age and obesity.

8. Group of *Truncilla rangiana* (Lea). (108 shells.)

(*a*) **Truncilla rangiana** (Lea).

*Unio rangianus* Lea, 1839. Obesity 44.4♀.

*Truncilla perplexa* var. *rangiana* Simpson, 1914. No measurement given.

(*b*) **Truncilla sampsonii** (Lea).

*Unio sampsonii* Lea, 1862. Obesity 58.7♂.

*Truncilla sampsonii* Simpson, 1914. Obesity 55.8♂; 64.5♀.

Lack of connecting material and of specimens of the more swollen form prevents making any statement as to the limits of these species, or as to their distinctness. There are only three clearly recognized *sampsonii* in the collection, and for these no locality is known. Besides being more swollen, *sampsonii* differs from *torulosa* in having the marsupial swelling of the female the same color as the rest of the shell. The locality given by Lea is the Wabash River, near Harmony, Indiana. *Sampsonii* is more obese than *rangiana;* the female of neither is dark green behind, thus differing from the *torulosa* group.

The figures for *rangiana* alone, show a slight increase in obesity in the larger streams. Also there is a very slight increase in prominence of tubercles in the larger streams, a difference so small that it is probably not significant. *Rangiana* is very poorly tuberculated. The male *rangiana* are more swollen than the female.

| Stream-flow | All shells | Male shells | Female shells |
|---|---|---|---|
| 0–749 | 48.667 | 50.0 | 47.5 |
| 750–1,749 | 47.838 | 47.905 | 47.333 |
| 1,750–3,249 | 46.476 | 47.739 | 48.681 |
| 3,250–8,249 | ..... | ..... | ..... |
| 8,250–25,249 | 49.889 | 50.154 | 49.2 |

For *rangiana* there is no correlation between obesity and age.

## Discussion

It should be noted in particular that because a correlation between degree of obesity and size of the stream has been found it does not follow that the stream size is the cause of the change in shape of the shell. It seems certain that other factors enter in; in fact, it may be that stream size has nothing to do with obesity except indirectly; that is, that other conditions besides size—conditions which, however, occur in large streams—are the direct cause. This seems probable when it is remembered that lake and canal forms are quite

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swollen, regardless of the size of the stream as measured in second-feet. In lakes and canals, big-stream conditions are duplicated except for size. In large streams the beds are usually of mud, and quite smooth; the water is apt to be softer and freer from mineral matter than in the headwaters (Ohio St. Bd. Health, 1898); the amount of silt is greater in large streams (Danglade, 1921); the kind and amount of food, as well as the temperature, are different in small and large streams (Grier, 1920*a*). Any or all of these conditions may be the ones which determine the character of the mussel fauna at any definite locality. Furthermore, the character of the pre-glacial drainage, as in *Amblema perplicata,* may influence the occurrence of intergrades.

Wilson and Clark (1914) suggest that the flatter forms are better adapted for crawling into the gravel and withstanding the strong current of small streams, and that the more swollen forms are better suited for the soft mud and weak current of large streams where greater inflation means more buoyancy. This suggestion is of doubtful value; it is hard to see how a difference in obesity of a few percent will increase the buoyancy of the shell to any appreciable extent. In fact, it is probable that rapidity of flow and the character of the bottom are not very important factors. Highly swollen shells occur in the Ohio River; yet the bottom for a good part of the distance is sand and gravel, and not mud at all. Furthermore, shells are quite apt to be found in riffles or on sand banks of the larger streams and not on the mud bottom or in deep water. Yet such shells are highly swollen.

It may be that the degree of obesity is not an adaptive character at all, but is merely connected with another character which may be adaptive or else more directly influenced by stream conditions. Isely (1913) has shown that little migration occurs among the mussels after they leave the fish; the *Lampsilis* group, however, tends to move more than the *Quadrulas.* This may explain the lack of correlation between obesity and stream-flow in many instances in the former group. It seems probable that migration, either before or after the parasitic stage, must occur, in some instances to a considerable extent, as in the case of the small streams entering the Tennessee near Florence, Alabama. Of course, other factors of distribution may have something to do with this phenomenon. The fact of greater obesity in youth for most shells indicates a differential growth-rate; shells do not tend to grow, each year, proportionately as much in diameter as in length.

Perhaps the most important question raised by this discussion is that of the heritability of these variations. If they are not inheritable, but solely the result of growth in a particular environment, how do the more swollen forms come to be found in the small streams which are tributary to large rivers; *e.g.,* near Florence, Alabama? Adult shells migrate very little. Furthermore, young shells, only a year or so old, are more obese in larger streams than shells of the same age in smaller rivers. Yet the effect of the environment on these young shells can not have been registered very noticeably in

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one year's growth. On the other hand, if these characters are inherited, how can one explain such peculiarities of distribution as that of *Ptychobranchus greenii flavescens,* a flat form, which occurs in the Black Warrior, the Cahaba, practically skips the Coosa, and turns up again in the Tallapoosa; though these rivers are all more or less parallel, empty into a common stream—the Alabama, and lie with the Coosa between the Cahaba and the Tallapoosa? Furthermore, why do the same size streams, though belonging to entirely different drainage systems, *usually* have shells of a comparable degree of obesity?

This is a question to be settled by experiment. Outside of Lang's work on *Helix* (Adams, 1915), practically nothing has been done experimentally on this phase of the problem of inheritance in molluscs. This is a field practically untouched, which promises excellent results for any one who enters upon it.

## Conclusions

For the species considered:

1. Shells of the same species often change in shape according to the size of the stream in which they occur. Shells of smaller streams are less swollen than those of larger streams.

2. Certain groups of shells show this correlation much more strongly than do others; in some cases there is apparently no relation between the size of the stream and the degree of obesity.

3. Other factors in addition to the size of the stream apparently enter into the determination of the degree of obesity.

4. For most species considered, young shells are more swollen than older ones.

5. There is frequently a correlation between sex and obesity; either the male or the female shell may be the more swollen.

6. In some cases the development of the tubercles is greatest in the large-stream forms; in other cases tubercle development is the same throughout the stream.

7. Usually the flattest and the most swollen forms are connected by a complete series of intergrades.

## Summary

In the opinion of many investigators, certain variations of fresh-water mussels are apparently not fortuitous, but depend upon various ecological conditions. A statistical investigation proves this to be the case in some groups. A comparison of stream-flow measurements with the obesity of shells belonging to a single species shows frequently that shells in large-size streams are more swollen than those of small-size streams. Since obesity is frequently used as a specific character, and since many so-called species can

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be connected by intergrades, this investigation has made clear that certain mussels, now considered separate species, are merely the different forms of a single species-group. However, it is probable that the size of the stream is only the indirect cause of any differences in obesity. Shells tend to become less obese as they grow older. Frequently one sex has a more swollen shell than the other. It is uncertain whether or not these variations, except those connected with sex, are inherited.

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# THE SIGNIFICANCE OF THE GREGARIOUS HABIT

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The gregarious habit occurs so frequently in nature as to indicate that it is an adaptation which must be of great biological significance. Considerable attention has indeed been given to this topic, but our knowledge concerning it is still far from complete, and even fragmentary contributions are not without their value. Certain studies of the habits of a gregarious bird which have been carried on by the writer during the past year (Miller, 1921) have suggested some ideas on the subject of the flock as an economic institution which may prove of more general interest than the limited scope of the investigation would seem to imply.

The Coast Bush-tit, *Psaltriparus minimus minimus* Townsend, is one of the most familiar passerine birds of the Pacific coast region, ranging through "Lower and Upper Sonoran zones of a comparatively narrow strip along the coast at least from the Oregon line south into northern Lower California" (Swarth, 1914, p. 510). It is a diminutive, drab bird, "top of head sooty brown; back dark grayish brown or brownish gray; under parts smoky brownish on sides. Length: 4.00–4.50 inches" (Bailey, 1917, p. 460). Peculiar, as the name suggests, to dense brush and chaparral, the Bush-tits forage about during the greater part of the year in loosely organized flock formation, which Grinnell (1903, p. 85) has admirably described as "a loitering company, scattered among several scrub-oaks or brush-clumps." These bands ordinarily consist of from fifteen to thirty individuals, but may occasionally number as high as sixty or seventy. Almost entirely insectivorous, they depend largely on scale insects and aphids for sustenance; various Lepidoptera and beetles, chiefly harmful, and some spiders, flies, and small wasps are also included in their diet (Beal, 1907, p. 74). Thus in their limited range, peculiar flock formation, and habits of feeding the birds occupy a place in the economy of nature which is unique.

The principal enemies of the Bush-tit are to be found among the smaller hawks, especially of the Sharp-shinned and Cooper species. The Sharp-shinned Hawk, *Accipiter velox,* does not soar and look for prey from above, after the manner of many hawks, but hunts actively through the tree tops where the smaller species of bird are likely to be found. Its method of striking is to dash through a tree, snatch a bird from its perch, and pass on without pausing. Thus its ecologic niche is such as to mark it as the Bush-tit's most formidable foe. Cooper's Hawk, *Accipiter cooperi,* is similarly a



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low flier, but, being a more powerful bird, it probably feeds upon Bush-tits only in the absence of larger prey.

The first and most obvious advantage of the gregarious habit is that it affords a multiplicity of eyes; the chances of sighting an enemy from afar are greatly increased; the alarm is sounded and measures for defense are taken. It is here that a further advantage of the flock over the individual becomes evident.

The reaction of a flock of Bush-tits to the approach of a Sharp-shinned Hawk or other avian enemy is extremely interesting. First, the most exposed birds sound the alarm and dash for cover. Those individuals feeding in the top-most branches are usually the first to perceive the danger; immediately they dart into the protection of the foliage, giving a shrill alarm note as they go. Then, as if by magic, the flock becomes stationary. Every bird is glued to its perch. Not a motion attracts attention to any particular individual. Simultaneously every throat gives utterance to a prolonged shrill, quavering note, the "confusion chorus" (Grinnell, 1903, p. 86), which, by its curious ventriloquial effect, renders the birds extremely hard to locate and distracts attention from any particular one. The flock remains thus motionless and the chorus is continuously uttered until the danger is past.

The effect of this upon a predaceous bird is obvious. Every sportsman knows that if he aims at a solitary water-fowl rising from the marsh, he is much more likely to bag his game than if he shoots recklessly into a flock. It is easier to hit a single bird than one of a dozen. The number of possibilities in the latter case distracts the attention from any one individual, and in consequence all are likely to escape. It may be stated as an axiom that the more the attention is divided, the greater is the possibility of failure. Now, in the case of the lower animals, the confusion arising from divided attention must be much greater than in ourselves. Animals appear to possess single track minds. They do not readily adapt themselves to puzzling circumstances. A dog may be taught to fetch a stick thrown by its master, but if two sticks are thrown at once, it is likely that neither will be brought. Division of attention means failure.

A hawk striking at a solitary Bush-tit would probably be successful in nearly every instance; but a hawk attacking a flock, every individual of which remains motionless, protectively colored and half concealed by foliage, no bird one whit more prominent than another, all uniting in a confusing cry, is likely to pass on without securing its intended prey. On half a dozen occasions I have seen a Sharp-shinned Hawk pass immediately over or through a flock of Bush-tits so reacting, without striking, although ordinarily it will kill in excess of its needs. It is extremely unlikely that mere caprice on the part of the hawk permitted the Bush-tits to escape. Rather it appeared that the predator was confused and unable to select a victim.

Of course, the hawk must sometimes be successful, or it would speedily

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grow tired of this game. Stragglers from the main flock are doubtless victimized most often. Theoretical computations based on the number of nestlings reared by a pair of Bush-tits each spring indicate a mortality rate of 250 percent of the minimum population. That is, for every 100 birds which survive from one breeding season to the next, 250 are killed, chiefly—as every ornithologist will agree—through the ravages of enemies, natural deaths being relatively rare among birds. But without a protective device such as the gregarious habit affords, the species would doubtless speedily become greatly reduced in numbers, or even exterminated.

Very interesting in this connection is an observation recorded by Allen (1920) on the behavior of sardines with reference to the attack of a loon. While the example is rather removed from the case we have been considering, the principle involved is identical. The loon made numerous dashes through a school of sardines, but came up each time without apparently capturing any of the fish; and Dr. Allen suggests "the possibility that the bird was unable to make a choice amongst so many chances before his opportunity was gone." It is to be noted that the striking feature of the behavior of the sardines was *uniformity*. Any departure from the stereotyped reaction would doubtless be fraught with immediate disaster. There is no room for originality. The individual is safe, not as an individual, but only as part of a group.

The advantage of concerted hostilities has long been recognized, but the evidence would seem to show that concerted pacifism or even concerted panic may be quite as effective as a measure of defense.

A further important advantage of the flock is to be found in its success as a foraging expedient. It represents the most economical method of range-occupation. Let us suppose, for purposes of illustration, that 100 birds of a given species occupy 100 acres of land as a forage ground. Three possible methods of procedure are open to them:

Every bird may roam at will over the entire territory, seeking what it may devour. Various individuals will cross each others' paths. One will forage unsuccessfully where another has been before him. All are likely to find scant fare. This method is unwise and wasteful; the greatest expenditure of time and energy is involved, with the least returns.

Another method, adopted by many birds, is that of apportioning off the territory by a sort of mutual agreement. Each bird will have a plot of its own, perchance an acre or so in extent, in which to forage intensively. Property rights are, of course, recognized very vaguely, if at all, but in a general way the individuals keep spaced out, so that there is little overlapping of forage grounds. This method, while a great improvement on the foregoing, is not ideal. Variations in the nature of the different portions of the territory thus occupied would be likely to give to certain birds an advantage over the others in matters of food supply and protection from enemies. Birds which chanced to occupy poorer portions of the range would fare badly.

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Both of the above methods involve competition. Under certain circumstances competition may be very desirable, but here it is wasteful and dangerous. The general struggle for existence is sufficiently keen to keep the species up to its highest level of development. Competition within the species is unnecessary and extravagant, and it puts a species which practises it at a distinct disadvantage. The species which substitutes cooperation for competition promises to be the most successful.

The flock organization of the Bush-tits represents the third possibility of range occupation. It insures that each individual shall share in the benefits of the entire forage range, yet without any wasteful crossing of each other's paths, as would be the case if each hunted alone. Time and energy are conserved. Moreover, multiplicity of eyes is here once more of advantage, meaning greater probability of finding food. Pycraft (1910, p. 136) observes of the Long-tailed Tit, an Old World species of similar habits:

"The vagrant bands . . . are held together very largely at any rate by their common needs. The discovery of insect food at this time is an arduous task, and if undertaken individually, many would starve. As Professor Newton remarks: 'A single titmouse searching alone might search for a whole day without meeting with a sufficiency, while if a dozen are united by the same motive, it is hardly possible for the place in which the food is lodged to escape their detection, . . . and a few call notes from the lucky finder are enough to assemble the whole company to share the feast.'"

This is the true socialism, nature's ideal political economy. The Bush-tits have all things in common, yet each is dependent on its own efforts for a livelihood. There are no overseers, yet there are no shirkers; necessity sees to that. No humanly devised Utopia has ever approached this in practicability. Each individual in striving for its own welfare unconsciously labors for the good of all. The success of the plan is due to the fact that it is entirely automatic and unvolitional, and not dependent upon any capricious altruism; consequently the element of selfishness does not invalidate it. If the food call is given, it is primarily because an individual has found food; only secondarily does this serve as a signal to its fellows. If the alarm note is uttered, it is primarily because some bird is alarmed; probably unintentionally this acts as a warning to its companions. Yet the summation of these individual acts, pure reflexes in many cases, is a mechanism by which the safety and well-being of the entire flock is promoted.

That the plan is successful in the case of the Bush-tits an observer may convince himself in a few hours' time. They are a dominant species. In the region about Berkeley they compose a strikingly large proportion of the avian population, and are certainly twice as numerous as any other species. In 27 published accounts of their occurrence elsewhere in California which have come to my notice, they are twelve times characterized as common or abundant. It thus appears evident that the Bush-tit is in this region our most

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common—hence most *successful*—bird, and doubtless so largely for the reasons that have been suggested.

## Summary

Observation of the habits of a gregarious species of bird has indicated that the flock is an adaptation possessing definite survival value:

1. The flock affords the advantage of a multiplicity of eyes, thus increasing the chances of sighting an enemy from afar.

2. The flock, by a uniform type of behavior on the part of its component individuals upon the approach of an enemy, tends to confuse the enemy by dividing its attention among a number of possibilities.

3. The flock represents the most economical method by which a given number of individuals can occupy a given forage range.

4. The Coast Bush-tit, a bird in which the gregarious instinct is highly developed, is demonstrably one of the most successful species in its range.

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# THE RELATION OF CLIMATE TO THE GEOGRAPHIC DISTRIBUTION OF CROPS IN THE UNITED STATES

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A study of the agricultural statistics collected by the Bureau of the Census, Department of Commerce, and of data published from year to year by the United States Department of Agriculture, reveals the fact that the staple, and even minor, agricultural crops of this country have a marked tendency to geographic segregation. When the intensity of production of the various products is graphically illustrated on charts or maps, there is a decided tendency for the various crops to group themselves into certain more or less definite areas, the boundaries of which are often rather sharply drawn. We find also that when we group all crops together certain sections show a decided preponderance of production.

The principal physical factors that influence localization of crops are topography, character of soil, distance from market, and climate. In the United States climate is the most fundamental, unalterable, and important, not only in influencing the geographic distribution of the crops grown, but also in determining the suitability of the land for agricultural purposes in general.

Only about one half of the land area of the United States permits of profitable production of crops by ordinary farming methods, the other half being unsuited for this purpose principally by reason of roughness, infertile soil, or unfavorable climate. For the country as a whole, nearly 75 percent of the total land area was classified by the census of 1920 as being unimproved.[1] About one fifth of the total amount, principally in the western half of the country, is too hilly or rough for cultivation, which leaves a large proportion unimproved for other causes than mere roughness. Much the greater part of this is unavailable by reason of unfavorable climatic conditions, principally insufficient moisture, although a considerable amount is used for grazing purposes, or for non-intensive agriculture by the employment of special methods, such as dry farming practices. The portion of the unimproved area located in the eastern half of the United States is comprised principally of lands under forest and cut-over, which are potentially agricultural, in so far as climate is concerned, although some of it, especially in the Appalachian Mountain section, is so rough or infertile as to be suitable only for growing

[1] Forest land is at present classed as unimproved. When land is under forest management and producing crops of timber—as much of it probably will be in the not distant future—should not some other form of classification be used? Ed.



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forest products. Most of this land is found in the northern portions of Michigan, Wisconsin, and Minnesota, and in the South from Virginia and the Carolinas to central Texas. Most of the unimproved land in the West is wholly unsuited for intensive agriculture, when unirrigated, owing to scanty moisture.

In a study of the relation of climate to agriculture two general divisions of the country are necessary. The first on a basis of moisture alone, and the other on that of temperature and rainfall combined, with the former dominating. In the first division we must consider agriculture in the composite—that is, from the standpoint of the general suitability of the land for growing crops of any kind, without the employment of special methods, such as so-called dry farming, or by artificially supplying moisture by irrigation. The second division is on a more concrete basis and subdivides the larger areas more or less specifically by crops, such as the corn belt, the cotton belt, and other similar groupings.

## Moisture Requirement of Crops

The amount of moisture required by crops for their best development varies for different localities and for different crops. The minimum amount of rainfall required under favorable distribution is usually considered to be between 15 and 20 inches of annual precipitation. Several modifying influences must be taken into account, however, which have wide geographic variations. Among these are soil texture as affecting its moisture-retaining qualities, temperature conditions, and rate of evaporation.

Broadly speaking, the 15-inch annual isohyet may be considered as the limiting line of our moisture division in the more northern portion of the United States and the 20-inch isohyet in the Central and Southern States, which conforms roughly to about the 101st meridian. Thus in our general division the country may be divided into two parts, the meridian mentioned roughly forming the dividing line. The total value of all crops grown in the United States in 1919 was nearly 15 billion dollars, about 90 percent of which was produced east of this meridian.

In a study of the amount of rainfall usually received in its relation to agriculture, the question of loss of soil moisture by evaporation becomes of much importance, especially in regions where the available moisture supply borders on the minimum limit for the successful production of crops, such as the sections we have just considered where the annual precipitation is from 15 to 20 inches. The rate of this evaporation depends principally on the soil texture, temperature, wind movement, and the relative humidity of the atmosphere, while the amount of moisture present and the loss by transpiration of vegetation are also important factors. It becomes, therefore, a difficult matter to determine by direct observation the loss of soil moisture by evaporation, and no extensive data showing this loss directly are available; but evaporation

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from a free water surface gives some indication of the relative loss from the soil for different localities. The amount of evaporation over the Great Plains region shows a pronounced and progressive increase southward from the Canadian border. The agricultural significance of these facts, stated in terms of actual equivalent rainfall, can be determined only approximately; but some investigations have shown that from an agricultural standpoint 20 inches of annual rainfall in eastern North Dakota is equivalent to about 30 inches in southern Texas. The 20-inch line of average annual precipitation extends in a north and south direction through the Great Plains region, conforming roughly to the 100th meridian of West Longitude. This line in North Dakota passes through a region where we find successful production of wheat, oats, timothy, and other crops characteristic of the humid type of agriculture; but in Texas it passes through a country devoted largely to grazing and the growing of drought-resistant crops, such as kafir and milo. Throughout the western section of the country evaporation from a free-water surface is much greater than the rainfall. At Yuma, Arizona, the evaporation from May to August, inclusive, is about 40 inches, while the normal rainfall is less than one inch for the same period; it is about 10 inches greater in southern Texas than in North Dakota.

In addition to evaporation, the seasonal distribution of precipitation is of prime importance. Where the rainfall is comparatively light and varies in different seasons of the year, it is necessary that the more generous amounts occur at a time when temperature conditions are favorable for vegetative growth. With an annual precipitation of only 15 inches, other conditions must be very favorable for profitable agriculture by ordinary methods. There are important grain sections in the more Northwestern States which receive on the average less than 15 inches of precipitation. In fact, in some localities wheat is grown where the normal annual precipitation is only 9 or 10 inches; but in such cases special methods for conserving the soil moisture must be practiced. In the great spring wheat region of the Red River Valley of the North, however, the average annual precipitation is only about 20 inches, and ordinary farming methods obtain.

Even with 20 inches of rainfall annually, if the amounts were uniformly distributed throughout the year, moisture would be insufficient for the production of most of the staple crops grown in the United States. We find in the great wheat-producing Plains region heavy grain production where the annual amount of precipitation is comparatively small. This has been made possible only by the favorable seasonal distribution of rainfall. There are a number of distinctive types of precipitation in the United States, and in this particular area the rainfall is characterized by generous amounts in the late spring and summer months, at a time when the moisture can be best utilized by growing vegetation, and by very light fall and winter precipitation. Owing to this fortunate provision of nature our moisture division line extends much

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farther westward than it otherwise would; and to this is due, in a large measure, the reputation of our western Plains States as a great grain-producing section.

Over a belt extending from Nebraska and Kansas eastward to Kentucky and Ohio a census classification shows about 66 percent of the total land area as improved, while to the northward from 30 to 45 percent is so classified, and to the southward from 16 to 40 percent. For the States of Montana, Idaho, Wyoming, Nevada, Utah, Arizona, and New Mexico the classification shows an average of only about 3 percent of the total as improved. While the topography of the latter area precludes a high percentage of improved land, deficient moisture is largely responsible for the very small percentage shown there, and ample moisture for the high percentages farther east.

From the standpoint of rainfall the United States is one of the most favored countries of the world. The vast expanse of comparatively level and fertile land extending from the Rocky Mountains on the west to the Atlantic Ocean on the east, and from the Great Lakes to the Gulf of Mexico, receives, as a rule, adequate moisture, and temperature conditions are mostly favorable for intensive agriculture. There are from time to time, it is true, rather severe and damaging droughts, and occasionally there is too much rain; but when either of these conditions obtains, the area affected is usually more or less localized, leaving sufficiently large favored sections to supply the nation with needful food, and some to spare; no famine specter thus far has ever disturbed us. However, there are large areas in our Western States comparatively unproductive that would greatly increase our agricultural output were sufficient moisture available. It has been estimated that about 30,000,000 acres of this semi-arid land is potentially irrigable, were all available sources of water supply fully utilized for irrigation purposes. This would provide over 300,000 additional farms. As the initial cost of developing irrigation systems increases with development of less favorable projects, the work will probably proceed rather slowly. At the same time large areas of relatively unproductive land in our Eastern States where climatic conditions are favorable are susceptible of improvement at a comparatively small expense, with the added advantage of being nearer the principal market centers.

## Temperature Influence on Crop Distribution

In studying the geographic distribution of specific crops, temperature conditions are found to have a greater influence than rainfall. In this case we shall consider only that section of the country east of the Rocky Mountains, or the principal agricultural area, in which precipitation is usually sufficient. The average summer temperature and the average winter temperature, especially the former, have a more direct bearing on crop distribution than that for the other seasons of the year. The agricultural provinces have more or less definite boundaries extending, in a general way, in an east-west direction

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conforming to the isothermal trend. A definite amount of heat is required to bring a crop to maturity. A rough measure of this may be obtained by temperature summation or what is known as the "thermal constant." This is the total, or accumulated, day-degrees of temperature in excess of some significant temperature taken as a starting point, computed to the date of maturity. The thermal constant of a particular plant and the temperature at which its growth may be started determines whether or not the temperature conditions in a given locality are favorable for its maturity. The planting of a given spring crop usually begins in the southern portion of the area in which it is grown and proceeds northward as the season progresses. There are certain restricted limits of time within which crops must be planted for best results, defined by the temperature conditions of the locality, and this period of time decreases in general with increased latitude. The planting and harvesting dates for the staple crops of the United States have been determined by the U. S. Department of Agriculture.[2] A study of these reports in conjunction with normal temperature conditions brings out some interesting facts. While the normal daily temperature at which planting usually begins differs for different plants, it is quite uniform for the same plant throughout the country. The seeding of spring wheat begins when the normal daily temperature rises to about 37° F., spring oats at 43°, early potatoes at 45°, corn at 55°, and cotton at 62°. Whether a farmer lives in the South or in the North, he has, unknowingly no doubt, adopted these temperatures as the proper ones at which planting should begin. Thus the planting of early potatoes, for example, usually begins in northern Mississippi about February 15, and in northern Wisconsin two and one half months later, but in each locality when the normal daily temperature rises to 45° F.

In a general way, we may divide crops into two classes, those known as cool-climate crops, more intensively grown in the central and northern sections of the country, and warm-climate crops, grown chiefly in the Central and Southern States. Among the former may be included potatoes, wheat, oats, buckwheat, flax, and most grasses; among the latter we find cotton, corn, rice, sugar-cane, and peanuts. While the most intensive production of both winter wheat and corn is found in the same area, one classed as a cool- and the other as a warm-climate crop, the former matures early in the season before the warmer weather of summer comes, while the most critical period of growth of the latter is the warm mid-summer season.

As an illustration of the grouping of certain crops in more or less limited areas, it may be pointed out that about one half of the corn produced in this country in 1919 was grown in 6 States: Ohio, Indiana, Illinois, Iowa, Missouri, and Nebraska. If to these we add 5 others, namely, Minnesota, the Dakotas, Kansas, and Oklahoma, we include an area that produced more than

[2] Baker, O. E., Brooks, C. F. and Hainsworth, R. G., "A Graphic Summary of Seasonal Work on Farm Crops," Yearbook, U. S. Department of Agriculture, 1917.

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70 percent of all the wheat and oats grown in that year. More than 70 percent of the white potatoes were produced in the Middle and North Atlantic and North Central States, and more than 90 percent of the sweet potatoes and practically all of the peanuts in the South. On the other hand, about 95 percent of the flax area is found in the Dakotas, Minnesota, and Montana, while more than three fourths of the buckwheat acreage is found in New York, Pennsylvania, and Michigan. Practically no cotton is grown outside the principal cotton belt, and four fifths of the domestic rice comes from Louisiana and Texas.

In a general survey of that portion of the country lying east of the Rocky Mountains, we find 5 more or less distinctive climatic provinces, which correspond to definite crop groupings. These may be designated the sub-tropical coast, the cotton belt, the corn and winter wheat region, the spring wheat belt, and the hay and pasture province.

*Sub-tropical Coast.* This section has a warm and comparatively equable climate, with an average winter temperature ranging from about 55° F. along the central Gulf coast to 70° in extreme southern Florida, and an average summer temperature of 80° to 82°. The principal crops in this province are winter truck, citrus fruits, sugar-cane, and rice. The winters are usually mild, although an occasional cold wave may be experienced; temperatures as low as zero have been recorded to the Alabama coast. The summer temperatures are appreciably tempered by proximity to the Gulf.

*Cotton Belt.* The northern limit of successful commercial production of cotton is determined almost entirely by temperature conditions. A mean summer temperature of about 77° F. is the limiting value, which corresponds to a frostless season of about 200 days. Along the northern margin of the belt the last killing frost in spring occurs on the average about April 10, and the first in fall about October 25. The mean summer temperature in the southern portion is about 82° F. The cotton plant grows successfully under a much wider range of precipitation than of temperature. In the cotton-growing States the average annual rainfall varies from little more than 20 inches in the extreme western portion to 55 or 60 inches in some eastern sections of the belt. Cotton is unfavorably affected by too much moisture perhaps as often, or more so, than from insufficient precipitation. May and June particularly are critical months, when cool, wet weather is detrimental. The thermal constant for cotton, computed from the normal daily temperature at the average date of planting to the beginning of picking, is about 1,900° F., compared with about 1,600° for corn in central Iowa and 1,800° in central Ohio. The difference in heat requirement of the two plants is greater, however, than these figures would seem to indicate. For it must be remembered that these computations are made on the basis of the beginning of cotton picking, while as a matter of fact, unlike corn, the ripening season continues long after the first bolls are open, and, for commercial success in production, tem-

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peratures must continue sufficiently high for some time thereafter to bring to maturity the late formed bolls. In addition, corn planting usually begins with a mean daily temperature of 55°, while cotton requires about 62° for proper germination, which means, in time, the better part of a month. Cotton forms about 60 percent of all crops grown in this belt.

*Corn and Winter Wheat Belt.* The principal corn and winter wheat belt extends roughly from the Ohio Valley States westward to the Rocky Mountains. The average winter temperature in this area ranges from about 40° F. in the southern portion to 15° in the northern, and the average summer temperature from about 78° in the south to 70° in the north. The average frostless season ranges from about 140 days in the north to about 200 in the south. The thermal constant for corn in the principal producing areas ranges from 1,600° to 1,800° F., computed as previously indicated. Along the northern limit of successful commercial production it is about 1,400°, but in some southern States, where slower maturing varieties are planted, it runs as high as 2,800°. It is interesting to note that in the more southern States there is a large excess of heat during the growing season over that required for maturing corn. For example, in southern Georgia the potential thermal constant for this crop, when computed from the accumulated day-degrees of temperature above the average at the time of beginning of planting to the average date of first killing frost in the fall, is over 4,000° as against 1,600° in central Iowa. This permits of successive plantings in the south covering a considerably longer period in the spring. That is to say, early, intermediate, and late crops can be grown.

*Spring Wheat Belt.* This belt lies mostly in the north-central section of the country, principally in the States of Minnesota, the Dakotas, and Montana. The average summer temperature along the Canadian border is about 65° F., while the southern boundary of the belt conforms approximately to the mean summer isotherm of 70°. This is by no means the northern limit of spring wheat production, however, as much is grown in the Canadian provinces farther north. In the United States the average frostless season of the belt varies from about 100 days in the north to about 140 days in the south. As in the corn and winter wheat belt, farming is rather diversified, but spring wheat forms more than one third of the crop acreage.

*Hay and Pasture Region.* This province is less well defined than the others mentioned and is, as a rule, a region of varied agricultural conditions. It includes mostly the northern border States from Minnesota eastward and extends to the Middle Atlantic States and Appalachian Mountain districts. The average summer temperature ranges from about 62° to 70° F., and the average winter temperature from 10° to 25° F. Climatic conditions in this province are favorable for the production of potatoes, buckwheat, and other cool-climate crops, but the dairy products predominate. They amount to about one half of the total for the United States.

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# VARIETAL DIFFERENCES IN THE RESISTANCE OF CABBAGE AND LETTUCE TO LOW TEMPERATURES

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There is a limiting zone of temperature for each of our crop plants beyond which it can not be grown without danger of failure from freezing. The temperature zones of our country are well known, and in many States the dates of earliest and latest frosts, as well as the minimum winter temperature, have been charted for a number of years. The temperature limits for the varieties of crop plants are by no means so well known. Most of our information is based upon the experience and opinion of farmers, and no accurate data are available on the low temperature limits which ordinary crops can withstand. The opinions of expert horticulturists vary greatly concerning the relative frost resistance of our most common varieties of garden vegetables.

Plants which do not withstand freezing of their tissues are limited to temperatures above their freezing points, but numerous important crops can withstand freezing if they are previously hardened. Small differences in the rate of hardening may determine the survival of varieties. It was the purpose of this study to determine if varietal differences in hardiness can be placed on an exact basis.

The winter resistance of cabbage and lettuce varieties has become of importance owing to their increased use as salad plants in early spring, and also on account of the gradual northward trend of the area over which they are grown in winter for the spring market. Studies on nutrition have shown that fresh green vegetables are necessary articles of diet. It is therefore desirable to have fresh salad plants available during as great a part of the year as possible. Every one is acquainted with the craving for "greens" in the spring. This craving is a sure indication of the insufficient use of these foods during the winter. The most effective way to supply this need is to produce salads for use in early spring. Cabbage and lettuce are especially adapted for this purpose on account of their high yield per acre and good keeping qualities which make them available at prices which can be afforded by all classes in contradistinction to greenhouse grown salads. Cabbage is a better keeper than lettuce and can be marketed in better condition, but it is highly desirable to have salads which will be used uncooked, and for this purpose lettuce is the favorite. The Chinese cabbages are very desirable for use as fresh salads, but unfortunately they are more susceptible to frost than ordinary cabbage. Some breeding must be done upon them before they can be made available for general use. Frequently cold winters such as occurred



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in 1919–1920 have caused heavy losses in the winter-grown cabbage crop in the region about Norfolk, Virginia. The loss during that winter has been estimated at one half of the crop. It seemed desirable, therefore, to make accurate tests of the relative frost resistance of cabbage and lettuce varieties.

Practical experience has shown that only a few varieties of cabbage are adapted for fall planting. In the Norfolk region the Jersey Wakefield and the closely related Charleston Wakefield have been found superior in winter resistance. Trials were made to determine the reasons for this superiority in winter resistance and to test out the relative importance of some of the factors concerned in hardiness. It was considered desirable also to find if there are varietal differences in hardiness which can be expressed with exactness.

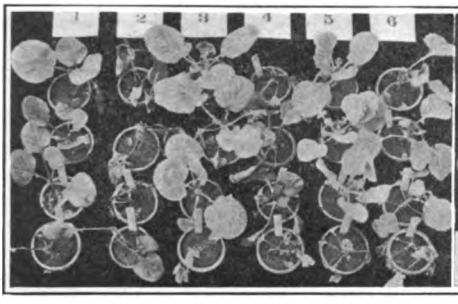

FIG. 1. Hardened 5 days at 5° C. Frozen 5 hours at —5° C. Front row greenhouse checks. No. 1, Mammoth Red; 2, Danish Stone Head; 3, Early Jersey Wakefield; 4, Zittauer; 5, Danish Ball Head; 6, Early All Season.

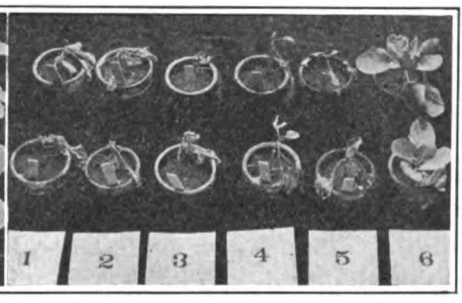


FIG. 2. Hardened 5 days at 0° C. Frozen 12 hours at —6.6° C. No. 1, Savoy; 2, Charleston Wakefield; 3, Danish Ball Head; 4, All Season; 5, New Early Succession; 6, Early Jersey Wakefield.

Field trials with plants in the open are undoubtedly valuable for the selection of winter resistant strains. But plants in the field have many factors to contend with, such as desiccation in the frozen condition, smothering from ice, and many other factors. It is therefore almost impossible to test out in the field small variations in any single factor such as differences in ability to harden. Furthermore, it is only seldom that temperatures are obtained which are of the proper range to make evident the differences in hardiness. The winter may be too mild to kill any variety, or it may kill all varieties. By using artificially controlled temperatures one can eliminate the action of many factors which would confuse the results of field trials. Also, one can adjust the temperature so as to select those plants which have a desired hardiness.

The author has used in this work four constant temperature chambers in which accurate temperature control was secured by electrical means, and low temperatures established by refrigeration. The chambers were provided for

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light exposure of the plants so that etiolation did not occur during the hardening period. Care was taken to eliminate differences in exposure of the plants.

There are undoubtedly many factors concerned in the ability of cabbages to survive the winter; but, above all, the changes which occur in the proteins whereby they are prevented from precipitating upon freezing is of the most importance. (I) Changes in the sugar content causing increased depression of the freezing point, or changes in the leaf coverings which aid undercooling of the tissue, are of less importance. (II) Red cabbages generally have a higher sugar content than the green varieties, with consequently greater depression of the freezing point. For this reason red cabbages do not freeze as quickly as green varieties, and unhardened red plants are not injured as easily as green cabbages which have been grown at the same temperature. But not all red cabbages harden well; that is, when exposed to temperatures somewhat above their freezing points, some red varieties do not acclimatize themselves to the low temperatures as quickly as some of the green varieties. This shows that the sugar content is not the deciding factor in frost resistance. The front row of plants shown in figure 1 are greenhouse controls and show the amount of injury to unhardened plants. The greenish-red Zittauer cabbage (No. 4, figure 1) does not harden as well as Red Danish Stone Head (No. 2, figure 1), and both of these are injured more than Early All Season (No. 6, figure 1), a green cabbage. The Mammoth Red variety (No. 1, figure 1) has a low freezing point at start and also hardens well, making it well adapted for winter resistance. Some green cabbages harden well, although they show but little frost resistance in the unhardened condition. This ability to harden is shown well by Jersey Wakefield (No. 3, figure 1) and Danish Ball Head (No. 5, figure 1). All plants shown in this photograph were of the same age and size. Except for those in the front row, they

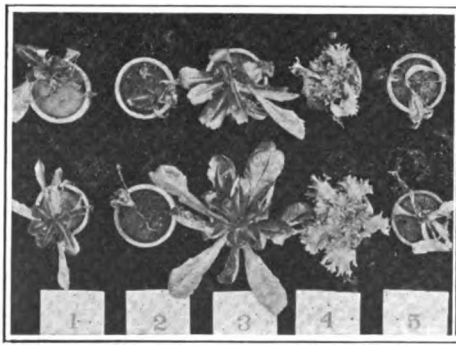


FIG. 3. Hardened 5 days at 3° C. Frozen 5 hours at —4.1° C. No. 1, Dreer All Heart; 2, Kingsholm Cos; 3, Hicks Hardy Winter Cos; 4, Boston Curled; 5, Hanson.

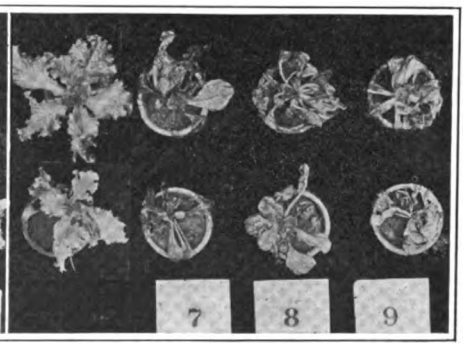


FIG. 4. Hardened 5 days at 3° C. Frozen 5 hours at —4.1° C. No. 6 (not numbered), Grand Rapids; 7, Brittle Ice; 8, Market Gardeners Private Stock; 9, Golden Queen.

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were all given the same treatment throughout. After growing to suitable size in the greenhouse at 60–65° F. (15.5–18° C.), those in the three upper rows were hardened in a constant temperature compartment for 5 days at 5° C. They were then placed with the controls from the greenhouse at —5° C. and allowed to freeze for 5 hours. They were then replaced in the greenhouse and allowed to stand for a few days so that differences in injury might become evident. The trials were repeated several times and effects were obtained essentially as shown in the photograph. In the series shown in figure 2 the plants were hardened for 5 days at 0° C. and frozen for 12 hours at —6.6° C. Under this more severe treatment the superiority of Jersey Wakefield (No. 6, figure 2) became evident. Greenhouse controls were all killed under these conditions.

Tests were made upon the Paoting, Peking, Shantung, Chosen, and Chokurei varieties of Chinese cabbage, but no differences in hardiness which would be of commercial value were discovered. The Paoting and Peking varieties seemed a little more susceptible to frost than the other varieties which have a tougher cuticle and whose leaves are less succulent. All of these Chinese cabbages are more susceptible to frost than the ordinary species of cabbages and do not harden well.

Tests were run upon lettuce to determine if varietal differences in hardening capacity exist in this group of plants also. In the fifty or more varieties of lettuce commonly grown by seedsmen a very great range of hardiness was shown. Many of these varieties are but little different in hardiness. In the photographs shown here selections were made of varieties which showed some contrast in their reaction to low temperatures. The order of injury for several varieties was found the same by numerous tests. Hence it is not necessary to put all plants of a great number of varieties under test at the same time. The relative order of hardiness can be established by placing a few indicator plants in each test. Usually two or three varieties which showed a range of hardiness were used as indicators, such as the very hardy Hick's Hardy Winter Cos and the less hardy Kingsholm Cos. From the amount of injury to such indicator plants in comparison with others in the series one can then make comparison between series.

In figures 3 and 4 the plants were hardened 5 days at 3° C. and exposed at —4.1° C. for 5 hours. Here Kingsholm Cos (No. 2, figure 3) is much more injured than Dreer's All Heart (No. 1, figure 3). Two curled varieties, Boston Curled (No. 4, figure 3) and Grand Rapids (No. 6, figure 4), hardened well. The order of increasing injury in this series is therefore:

Hicks Hardy Winter Cos < Boston Curled < Dreer's All Heart = Grand Rapids < Kingsholm Cos = Market Gardeners Private Stock < Golden Queen = Brittle Ice = Hanson.

In the tests shown in figures 5 and 6 all the plants were hardened for

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3 days at 3° C., a very short period, except the first row, which consists of controls from the greenhouse. They were exposed to —4.7° C. for 3 hours. From the first row of controls it is seen that Hicks Hardy Winter Cos (No. 1, figure 5) and Boston Curled (No. 1, figure 6) possessed considerable original hardiness. That is, they seem able to withstand the low temperature exposure without the preliminary hardening treatment. They are resistant to

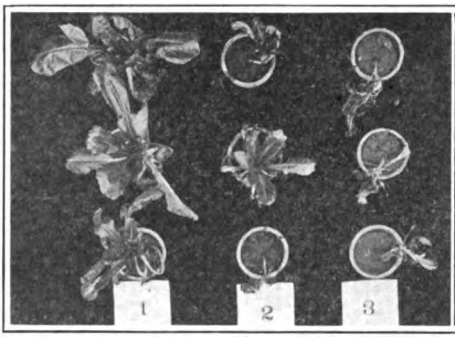


FIG. 5. Hardened 3 days at 3° C. Frozen 3 hours at —4.7° C. Front row controls. No. 1, Hicks Hardy Winter Cos; 2, Kingsholm Cos; 3, Giant White Cos.

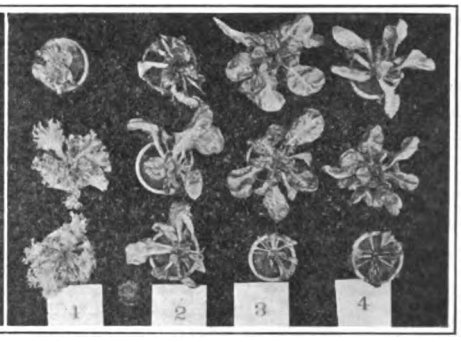


FIG. 6. Hardened 3 days at 3° C. Frozen 3 hours at —4.7° C. Front row controls. No. 1, Boston Curled; 2, Market Gardeners Private Stock; 3, Wayahead; 4, Defiance.

freezing, although grown at 55–60° F. (12.8–15.6° C.) in the greenhouse. The order of injury after hardening and freezing in this series is Hicks Hardy Winter Cos < Boston Curled = Wayahead = Defiance < Market Gardeners Private Stock = Kingsholm Cos < Giant White Cos. The order of injury is about the same as in the previous series. Some irregularities were observed such as the greater injury to one Boston Curled plant (No. 1, figure 6), the reason for which is not apparent. By making comparison between greater numbers of plants of each variety than are shown in this photograph these individual differences could be averaged. With the size of chambers used this would have limited the number of varieties to two or three for each test.

## DISCUSSION

It is evident from the data here presented that we have a valuable means of accurately determining the ability of plants to harden. The author believes that this method ought to be used in breeding work in which hardiness is the character desired. The method will undoubtedly allow the selection of those members of a cross which possess the desired degree of hardiness. Furthermore, small differences in hardiness can be detected which would not be noticed in field trials. By making use of artificially controlled temperatures it is not necessary to wait through a period of years to determine the hardiness of varieties.

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It is suggested by this data, and from previous work, that the ability to become immune to freezing at a given temperature is an expression of varietal differences in the protein constituents of the protoplasm. This property is not dependent upon the tendency of the variety to produce sugars which tend to decrease the precipitation of proteins on freezing. Cases have been mentioned in which high sugar content of a red cabbage did not render it less susceptible to freezing than green cabbages with less sugar; and, on the contrary, cases are given in which plants with low sugar content were more capable of hardening than those with high sugar content.

## Summary

An exact method for testing the ability of plants to harden is given and applications for it are suggested.

Using this method, the relative injury to varieties of cabbage and lettuce at low temperatures is shown to be dependent upon varietal differences in the ability of these plants to harden.

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# OBSERVATIONS ON SURFACE DISTRIBUTION OF MARINE DIATOMS BETWEEN SAN DIEGO AND SEATTLE

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In June, 1920, Dr. G. F. McEwen, while on a voyage from San Diego to Seattle and back, made a number of surface hauls of from two to five gallons of water from the decks of the passenger steamers. In connection with this work and with that of collecting water samples he secured the attention and interest of Mr. J. R. Mortensen, Second Officer of the steamer *Queen* of The Admiral Line, who volunteered to take similar collections for the use of the Scripps Institution at such times as he might be able to find. In the six months from July to December, inclusive, he was able to make a total of sixty-six collections of phytoplankton fairly well distributed as to both time and locality. The collections taken by Dr. McEwen totaled one hundred and one, and were taken at hour or half-hour intervals when it was found convenient in the two or three days actually spent at sea. In both series catches were made by the simple process of throwing a canvas bucket into the water, hauling it up and pouring the water thus secured through a filtration net of number 25 bolting silk. Most of the samples of water from which the catches were taken were small (two or three gallons), hence the catch was made with so few casts of the bucket that the ship had not made much progress during the hauling. For this reason sampling was fairly indicative of surface distribution of organisms in the immediate vicinity of the catch.

Enumeration was done by a modified Sedgwick-Rafter method. Estimates were recorded in number of specimens per liter. The records were then tabulated according to areas based on prominent localities, each area being about sixty to one hundred miles in length parallel to the coast line. Fourteen such areas were designated as indicated on the accompanying map.

Each of these fourteen areas showed at least a few diatoms in all or nearly all of the catches made by Mr. Mortensen, but in the more frequent catches made by Dr. McEwen on the single round trip there were eleven barren catches taken in the areas between Point Cabrillo and Cape Disappointment. On the other hand, some of the fifty productive catches in this area were very large.

Thirteen species of diatoms were recorded for the Mortensen series and thirty-three species for the McEwen series, the two lists being identical as far as the former goes. A few of the names are merely catch-all designations for unrecognized species or those represented by very small numbers. Most



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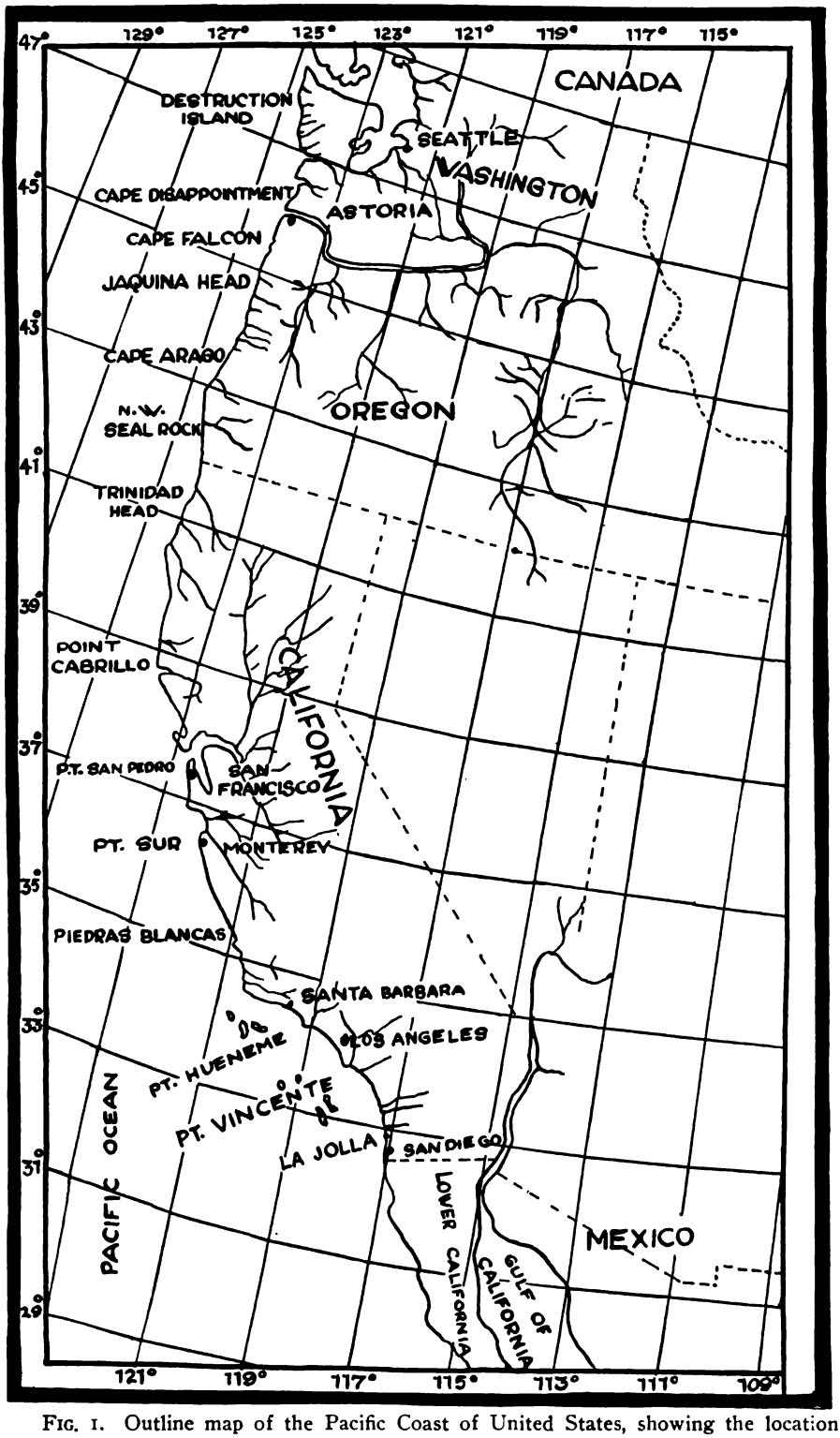


FIG. 1. Outline map of the Pacific Coast of United States, showing the location of the points mentioned in the text from which the catches were obtained.

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of the species in the final record are capable of identification without much error. All of them were found in three or more of the areas mentioned.

In the Mortensen series only two genera, *Chaetoceras* and *Nitzschia,* were very prominent at any time, but in the McEwen series *Eucampia, Skeletonema,* and *Thalassiothrix,* though not reaching large numbers, were represented in sufficient quantity in some catches to deserve particular mention. This difference in the two series is partly explainable by the greater number and greater frequency of the catches by Dr. McEwen, but it is probably more distinctly due to the fact that most of Mr. Mortensen's catches were made in the poorly productive period of fall and early winter. A similar difference is discernible in the case of species of the genus *Chaetoceras,* for which only three forms reached notable prominence in one or more catches of the Mortensen series, while eleven forms reached considerable prominence in the McEwen series. But the records show that the prominence of these eleven species appears mostly in single catches which might very probably have been missed in the long and irregular intervals between Mr. Mortensen's hauls; hence, while greater frequency would adequately explain the prominence of *Chaetoceras* forms in the McEwen series, we know that the favorable season is mainly responsible.

Ten genera were listed in addition to those just named above, but no catch greater than 3,000 was taken of a single species in any genera at any point. The genera *Chaetoceras* and *Nitzschia* were the only ones which were represented by individual species in more than one fourth of the catches. In the McEwen series maximum catches of sixteen out of the thirty-three species listed were taken south of Cape Mendocino, which is near the northern border of the area I have designated as the Point Cabrillo region. This is the section in which there is greatest upwelling of colder waters and it is near the point at which the main body of the Japan current is carried well away from the shore. Hence it appears to be a natural point of division between southern and northern waters of our Pacific Coast line. Seventeen species yielded maximum catches north of Cape Mendocino. Furthermore, the maximum catches in both northern and southern directions were almost all distinctly larger than any catches of the same species which were taken respectively south or north of the cape. Five of the exceptions were to the south and one to the north. The latter has been found in pier collections as far south as Pt. Hueneme (see map, page 141), and it is quite probable that the other five might be found to the north if the number and continuity of catches was sufficient. From the limited evidence before us we can only conclude that so far as geographical range of species is concerned there is no very marked difference in the diatom flora throughout more than a thousand miles of Pacific coastal waters. As to quantity, the showing is somewhat different. Both the Mortensen and McEwen series show maximum catches of total diatoms in waters near or north of Cape Mendocino. Both series also showed

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a distinctly higher average of catches of diatoms in the northern section—*i.e.*, 56,056 as against 4,535 per liter in the Mortensen series and 139,294 as against 77,245 per liter in the McEwen series. In spite of the small amount of evidence furnished by two such short series as these, it seems fairly clear that the area north of Cape Mendocino is, on the whole, a much more productive area in a quantitative way. Since this conclusion agrees with conclusions reached by many observers in regard to other oceanic waters of northern latitudes, it may be regarded as certain that more northerly waters generally produce larger quantities of diatoms.

Less definite indication of greater productivity in northerly waters is given by the following points: In the Mortensen series 5 out of 30 catches north of Cape Mendocino exceeded 40,000 per liter, while to the southward only 2 out of 36 catches reached that number. In the McEwen series 16 out of 61 catches northward exceeded 40,000 and 10 out of 40 to the south exceeded it. Also the Mortensen series showed 9 out of 30 catches north and 9 out of 36 south to be in excess of 5,000 diatoms per liter; and the McEwen series showed 22 out of 61 catches north and 25 out of 40 south to be in excess of that number. From such records it would appear that the ratio of catches above a certain number is essentially the same in both regions, but that the northerly region has a larger percentage of catches which run far in excess of that number. Or we may say that it seems probable that when conditions in a locality are favorable to a certain degree of productivity the tendency is for northern localities to carry production much farther beyond that degree than is the case in southern localities. And, indeed, this is what we might expect from the generally accepted view that diatom production is favored by a certain proximity to land from which there is any considerable drainage. The vastly greater contributory drainage in northern waters on our Pacific coast should have some such enriching effect as is indicated by the above-mentioned differences in production in northern and southern sections.

Such records as we have available at the present time give little indication as to the influence of various physical and chemical factors involved on the questions of distribution in this series of collections. In the Mortensen series no catch yielding more than 5,000 cells per liter was taken in water of a temperature less than 54° F. or greater than 60° F. On the contrary, the largest catch (numerically) taken by Dr. McEwen was in water of the lowest temperature recorded in his series. This catch was made about ten miles south of Cape Mendocino and it consisted almost entirely of *Chaetoceras sociale* Lauder, characterized by very small cells very difficult to estimate (much less count), and a form rarely found in any collections made by our institution. However, the largest catches made in some other areas were taken from points showing lowest temperature for those regions at that time. Hence it seems likely that regions of upwelling water or influenced by drift of upwelling water may be exceptionally productive under some circum-

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stances, and that a relatively wide range of temperature does not necessarily mean poor production. While we know that temperature is a most influential factor in all productive activity of living things, we are not able to say anything definite as to the mode or extent of its influence in diatom production.

In the Mortensen series only four areas seemed to be very productive. In order of numerical production these were Jaquina Head, Destruction Island, Pt. Cabrillo, and Pt. Hueneme. In the McEwen series they were Pt. Cabrillo, Destruction Island (including some catches inside the Straits east of Cape Flattery), Pt. Hueneme, Pt. San Pedro, Cape Disappointment, and Trinidad Head. In both series North West Seal Rock area seems to be very poorly productive and the McEwen series indicates the Jaquina Head region to be so, although it was most productive in the Mortensen series. Such facts serve to again emphasize the need of caution in stating conclusions about plankton production anywhere without long, continuous, and careful observations. As a matter of fact, the region of North West Seal Rock may be highly productive in certain years or certain seasons so far as we have any means of knowing at present.

Out of the innumerable questions always arising in connection with any study of marine life the following appear with especial prominence at this time, and for them we have no satisfactory answers:

1. Does productivity in deeper strata of the same waters vary in the same way as does that of the surfaces at the times of sampling or at any times? It probably does not, but we lack the complete evidence that it does not.

2. How is productivity at one place related to productivity at another? Did the highly productive areas in these series appear highly productive because certain plant foods were carried into them from others which by strong currents were thus kept non-productive, though contributing to productivity in other places?

3. Is high productivity in certain areas due to proximity of suitable breeding grounds for fish which produce the plant foods which in turn provide for their own feeding—*i.e.*, is it due to the fact that the organic cycle or circuit is completed in some areas, but not in others? There are vast numbers of minor questions leading from this.

4. If northern waters tend to be more productive, why did the Pt. Cabrillo and Jaquina Head areas show more fertility than the areas farther north in their respective series?

5. What was the extent of productivity in localities intermediate to those sampled at the time of sampling?

6. What was the extent of productivity at such times inshore, further off shore, and in deeper or shallower waters?

Fully satisfactory answers to such questions can be obtained only by colossal expenditures of time, money, and labor.

But in spite of the fact that so many highly important problems press

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vainly for solution it does appear that the study of this series of collections shows some points worth noting. These may be briefly stated as follows:

1. This evidence favors the generally accepted view that phytoplankton organisms are more abundant in northern waters.

2. It gives strong indication that certain areas are more productive than others, and that some may be highly productive at one time and poorly productive at another time within the productive season.

3. It shows decrease of production in all areas as winter approaches.

4. It shows that the region of prominent upwelling may be highly productive, at least at times, and that a temperature several degrees colder than that of adjoining waters does not prevent large production.

5. It indicates that our more prominent diatoms may exist or possibly flourish in surface waters of all areas sampled.

6. It suggests the probability that a limited series of collections of high frequency like those of Dr. McEwen may be almost invariably more valuable from the ecological standpoint than a discontinuous series carried over longer periods of time, but that the value of either or both may be very much increased by use of the other for comparison.

7. It shows that material obtained through use of commercial shipping may be highly valuable, and it indicates that there are important undeveloped possibilities of systematic work to be carried on through the use of commercial or naval vessels.

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# VARIATION IN THE DOG WHELK, THAIS (PURPURA AUCT.) LAPILLUS

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## INTRODUCTION

This paper is the second of a series on the local distribution of varieties of a species of mollusk in which there is a complete mingling of the races over wide areas. It is a study of mixed populations. Gulick (1905) on the *Achatinellidae,* Pilsbry (1912) on *Liguus,* Crampton (1917) on *Partula,* and others have described the distribution of mixed colonies and pure races of mollusca separated by barriers.

*Thais* (Purpura) *lapillus,* the purple sea snail or dog welk, has long been distinguished as the most variable member of the littoral formation of the north European and New England coast, and indeed, with its Pacific homologue, of the littoral formation of the whole boreal region. The skeleton or shell is variable not only in color, but also in size, thickness, shape, and sculpture. The variations are so great and striking from one locality to another that if some one with a complete knowledge of the *Thais* fauna were lost in a fog and landed on the shore he could at once determine where he was by an examination of the shells on the rocks.

## FACTORS INFLUENCING DISTRIBUTION

Without analysis by means of pedigree cultures we can sometimes recognize in a population two classes of variation: (1) Variations caused by the direct effect of the environment and not inherited; (2) variations caused by the chance combination of genes in the germ plasm which are inherited. We will refer to the former as environmental variations and the second as hereditary variations.

Can we distinguish environmental variations from hereditary variations by purely observational methods without recourse to experiment? This seems possible in some cases. If all members of a population differ in some character from those of another population subjected to different external conditions with no impassible barrier between, we can be pretty sure we are here dealing with an environmental character. If, on the other hand, we find individuals living side by side under the same external conditions which differ decidedly from one another in some character, we are safe to assume that we are here dealing with an hereditary character.



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The present paper records an endeavor to discover the kind of variation, that is, whether the varieties are due to direct effect of environment or due to hereditary factors. Moreover, the paper will present evidence on which the distribution of certain variations can be explained.

The solving of these problems has been limited to the method of direct observation, and several factors must remain undetermined until the methods of pedigree cultures can be applied.

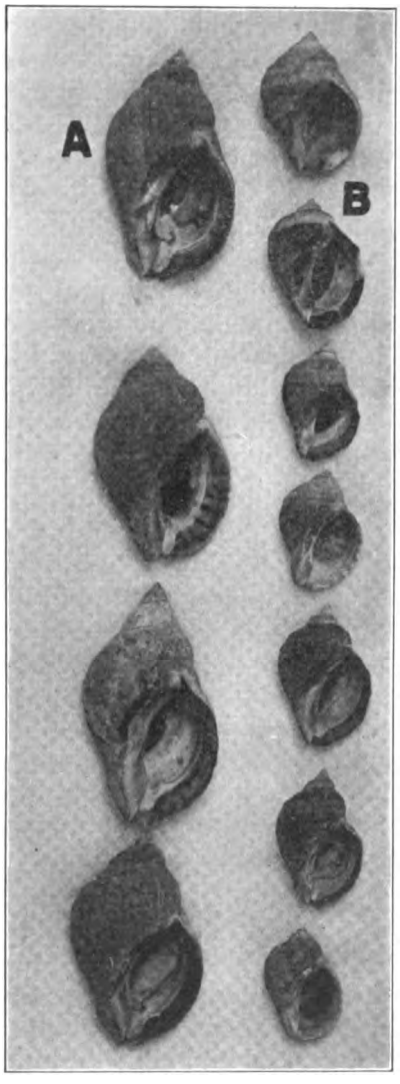


FIG. 1. Shells from the exposed coast, *B*, compared with those from sheltered harbors, *A*. An examination of large series of such shells indicates that the shape and weight of the shell is a direct reaction to the environment.

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## Habits and Habitats

In a previous paper (Colton, 1916) the author described the life history of this form and the relations of the animal to its organic and inorganic environment. In the present case it is necessary to recall a few of the conclusions because they have a bearing on the distribution.

The habitat of *Thais* is determined by the abundance of food, freedom from enemies, and nearness of hibernating spots. In the summer *Thais* lives between the tides on rocky exposures, with the barnacle, *Balanus balanoides,* or the mussel, *Mytillus edulis,* forming the chief foods. In places where enemies in the form of fish and birds are destructive *Thais* takes refuge in deep cracks in the rocks. Moreover, on rocks far from the water at low tide, such as in coves, even with food in abundance *Thais* is not found. Coves which freeze up in the winter time are not fit habitats for the welk. This means that the distribution of *Thais* is limited by food, enemies, and topography.

The normal dispersal of *Thais* is limited to its ability to crawl. At no time in its life history does it have a pelagic stage. As soon as the young hatch they hide in cracks in the rocks, where, feeding on mussel fry, they grow to adults. It is conceivable that waves sometimes dislodge them and roll them some distance; yet normally the evidence points to their travelling in their lifetime but a hundred feet or so from the place where the eggs were laid. Yet the same varieties are found on both sides of the Atlantic Ocean.

## Varieties of *Thais*

The conspicuous variations in *Thais* are all concerned with the shell: shape, size, sculpture, and color. These variations in the shell, of course, are reflections of variations in the cells of the mantle which secretes the shell. The spire may be tall or short; the size is large in some habitats and small in others; the shell surface may be smooth or it may have ten distinct ridges. In some cases alternate ridges become reduced or obliterated, giving the shell six distinct ridges (figure 4). The most striking variation of all is one called *imbricata,* in which the ten ridges become fluted. Experience seems to show that all of these varieties grade into one another, but the extremes are so striking that it is a wonder enthusiastic individuals have not given them appropriate names.

## Influence of Exposure on Size of Shell and Width of Aperture

Shells collected from an exposed coast subject to the pounding of the surf are all small and rather thin. Those collected from stations with plenty of food in sheltered bays are large and strong (figure 1). In the former case the aperture is relatively wide (ratio, height to width $= 1.32 \pm .004$); in the latter case the aperture is relatively narrow (ratio, height to width $= 1.70 \pm$

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.009). The greater area of the foot (aperture) of those exposed to the surf is a direct reaction to the environment in preventing the animal from being destroyed by the surf. Since there is no overlapping of these characters, it is evident that we are here dealing with the direct effects of environment.

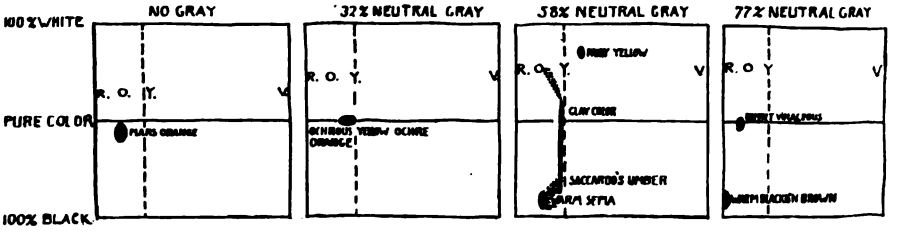


FIG. 2. The black spots indicate the distribution of the colors of *Thais lapillus* on the color chart of Ridgeway (1912). The chart seems to show that certain colors seem to offer a continuous series, but others are widely discontinuous.

R = red, O = orange, Y = yellow, V = violet, on the chart.

Shaded areas indicate where intermediates occur.

## THE COLOR VARIETIES

More conspicuous than the sculpture characters are the color varieties. In describing these the author has had recourse to Ridgway's Color Standards (Ridgway, 1912).

*Mars Orange.* A red variety found only at St. Andrews, N. B.

*Ochrous Orange and Yellow Ochre.* Yellow varieties widely distributed, but rarely abundant.

*Clay Color, Cinnamon, and Saccardo's Umber.* Pale brownish shades widely distributed and abundant in some sites.

*Warm Sepia.* A purple brown, most common of the dark varieties.

*Warm Blackish Brown.* A dark purple, fairly common on mud flats and rare on other sites.

*Russet Vinaceous.* A pale purple shell very rare, absent from most sites, but forming one or two percent of the population in a few places.

*Ivory Yellow.* A white shell colored a pale greenish yellow within the aperture, fairly abundant.

*White.* Pure white even within the aperture, absent from some sites and very abundant in others.

All of these varieties are quite distinct and offer a wide distribution on the color chart (see figure 2).

Not only do differences in color exist, but also the distribution of the color on the shell takes distinct patterns. Although many of the shells are self-covered—that is, the color is uniformly distributed—yet the lip may be white or banding may be conspicuous.

The banding exists in two forms, wide bands and narrow bands, which

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involve the ridges on the whorls. In the wide stripe two spiral bands of white encircle the shell. The width of the stripes is somewhat variable, so that the white bands either include ridge number 4 alone or numbers 3, 4, and 5, and either number 8 alone or numbers 7 and 8.

The narrow stripe variety has every alternate ridge white, forming five to seven white bands on a colored background. In some shells these two patterns are superimposed, which results in an almost white shell with four narrow bands of color. This is shown in the following table:

TABLE I. *Arrangement of Color Stripes*

W = white stripe, D = dark stripe

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Ridges |
|---|---|---|---|---|---|---|---|---|---|---|
| W | D | W | D | W | D | W | D | W | D | W | Formula for narrow stripe |
| D | D | W | W | W | D | D | D | W | D | D | Formula for wide stripe |
| W | D | W | W | W | D | W | D | W | D | W | Formula for combined effect |

A white lip within the aperture is characteristic of some shells in the Mt. Desert region, while at Rye Beach, N. H., the columella is white with a conspicuous purple spot.

## DISTRIBUTION OF COLOR VARIATIONS

Observation seems to show that certain color variations are independent of one another, so that many combinations are possible (Colton, 1916). Not all have been realized, however, for the possible combinations are about one thousand, and certain ones like clay color and warm sepia make up over half of the total population and but 16,000 shells have been collected.

## COLOR VARIATION AND BACKGROUND

Since differences in color are mixed in given habitats we must consider that they are due to heredity. If this is so, how does it come about that the varieties appear in such different proportions in different stations and are not evenly distributed?

Although the yellow shells appear more abundantly on yellow-colored rocks, as was first pointed out by Blaney (1906), and the red shells have been found by the author nowhere else but on the red shales at St. Andrews, N. B.—neither at Grand Manan nor in the St. Croix River—yet the numbers are small and the backgrounds have not been carefully studied. The inference is strong, however, that natural selection has here preserved those conspicuous forms which on other backgrounds are picked off by birds at low tide and by fishes at high water.

The effect of natural selection becomes more clear when the distribution of the light individuals is contrasted with dark. Greenings Island, a small island at the mouth of Somes Sound, furnishes a good example (figure 3). The eastern end is rocky and washed by clear water. On the upper rocks, which

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are of black basalt, the snails feed on the white barnacles. On the lower rocks, near low tide they feed on the mussels which are black like the rocks; 61 percent on the upper rocks are light colored; 37 percent on the lower rocks are light colored. The few rocky outcrops on the western end of the island are separated from one another by mud flats. On the rocks in this region barnacles are not abundant and where present are often covered with sediment and are therefore mud colored. Here the sea snails feed mainly on the dark-colored mussels, but 3 percent to 7 percent of the shells are light colored. The proportion of dark colors evidently is determined by the background.

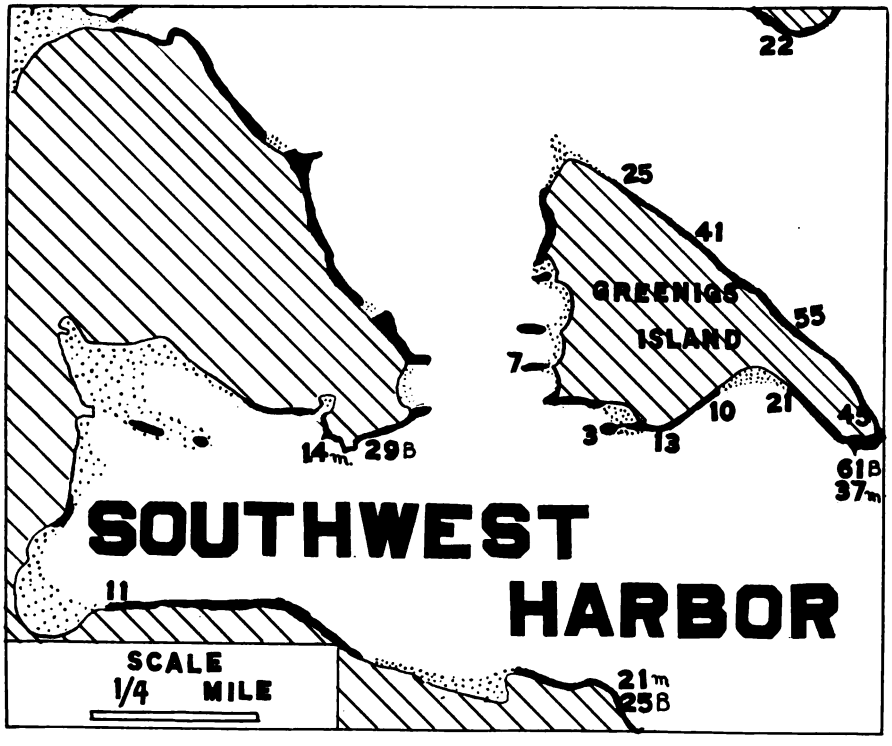


FIG. 3. Map of Greenings Island, Maine. The percentage of light colored shells is shown in figures on the various stations. On two sites collections were made close together but on different zones. "*M*" refers to *Mytillus* (mussel) zone, "*B*" to *Balanus* (barnacle) zone. The map makes clear the gradual darkening of the populations from the exposed eastern end of the island to the sheltered western end.

In other words, although the germ plasm of the populations contains the determiners for nearly all the varieties, yet a weak natural selection eliminates most of the conspicuous forms. We must assume that in some places the selection is rigorous, the conspicuous forms are all eliminated; in others it is not efficient, the conspicuous forms appear occasionally; or not acting at all,

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conspicuous forms are as abundant as the non-conspicuous forms. We must assume this, otherwise all conspicuous forms would disappear and the race would be homogeneous for each locality.

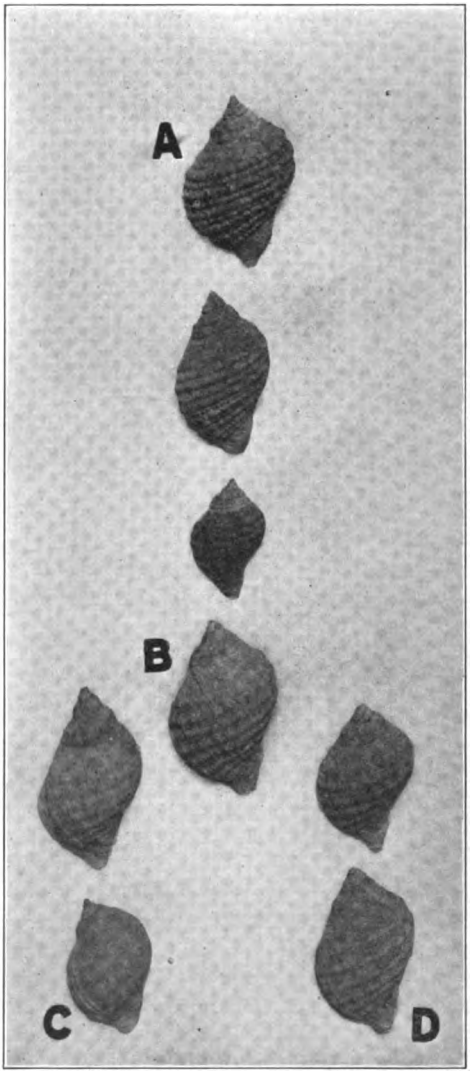


FIG. 4. A series of shells from the same station at Salisbury Cove, showing the continuous nature of the variation in sculpture. On the top we see the ten-ridged, fluted form *imbricata, A* melting into the typical *lapillus, B,* which grades into a smooth type, *C* on the one hand, and into a six-ridged type on the other.

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## The Variety *imbricata* of Lamarck

The three variations in sculpture of the shell of *Thais lapillus,* smooth, ridged, and fluted, grade into one another, yet the extremes are quite distinct (figure 4). Smooth grades into ridged, ridged grades into fluted. This fluted form was described by Lamarck as a separate species, called *imbricata.* On certain rocky shores of Mt. Desert Island, Maine, it constitutes as much as 93 percent of the *Thais* fauna, and on other sites not one specimen has ever been found.

Two bays wash the shores of Mt. Desert Island, Blue Hill Bay on the west and Frenchman's Bay to the east, while the southern shore is pounded by the surf of the Gulf of Maine. An indentation of this southern shore, guarded by a number of small islands, pushes itself north ten miles in a narrow fiord, cutting Mt. Desert Island nearly in half. This fiord bears the name of Somes Sound (see figure 6).

If we study the distribution of the imbricated variety in Blue Hill Bay, we find that the fluted forms are most abundant near mud flats. Indeed, in the whole Mt. Desert region there are but two sites out of ninety where a large fluted proportion is found over half a mile from a mud flat. If perfect correlation is 1 and no correlation 0, then the correlation of the sites where *imbricata* is found to mud flats is .95. In other words, the coefficient of correlation is high.

A strip of shore a mile long was studied in detail. This strip separated two stations where the proportions of *imbricata* in the population differed greatly: 4 percent at one point and 49 percent at the other (see figure 5). It shows very beautifully the correlation between mud flats and fluting: how very few fluted forms lived on the rocks washed by the waves of the bay while in the sheltered coves nearly half the population was fluted.

Although in Blue Hill Bay, on the west of Mt. Desert Island, *imbricata* is abundant, forming 20.5 percent of the total population (4,804 individuals) and ranging from 0 percent to 96 percent of the population at different sites, depending on the proximity of mud flats; yet in Somes Sound nearby they form but 1.1 percent of the population (10,102). Eighty out of the 112 forming the 1.1 percent were from one site. Moreover, on no site does the proportion exceed 19 percent, nor is there any significant correlation between mud flats and the presence of the form. The coefficient of correlation is but .35.

This contrast between the abundance of *imbricata* in these two nearby bays is so striking because both bays have the same kind of muddy coves. Other differences that might indicate differences in physical or chemical conditions are not apparent in the fauna.

## Factors Influencing the Distribution of *Thais lapillus imbricata*

As mentioned on page 146, it is possible to distinguish, in certain cases,

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variations caused by the direct effect of the environment from variations caused by hereditary factors. If we apply these tests to the variety *imbricata* and find that 93 percent are *imbricata* in Goose Marsh Cove, and five miles across the land at the head of Somes Harbor, just as muddy a cove, we find

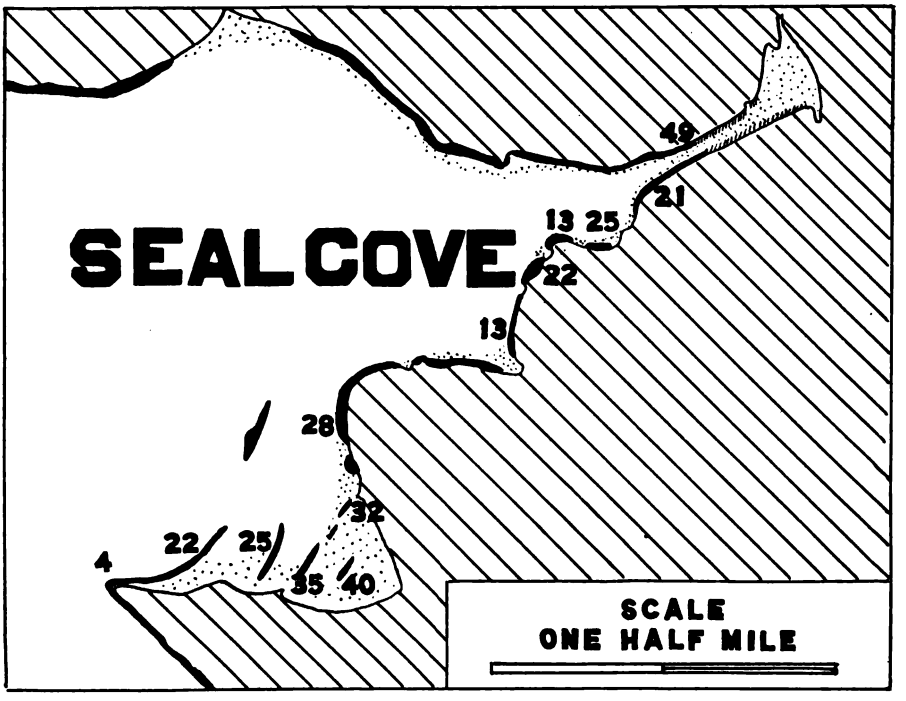


FIG. 5. On this map of Seal Cove is shown one mile of shore on which populations of *Thais* have been studied. The numbers refer to percent of *imbricata,* the form with the fluted shell. It will be noticed that on the outer point the number is but 4 percent, while at the head of the cove it rises to 4.9 percent.

that .6 percent are imbricated, the fluting can not be due to the direct effect of environment. This condition is repeated over the entire area. The imbricated variation, although a case of fluctuating variation in the sense of Darwin—intergrades can be found connecting it with smooth—is clearly due to an inherited factor or factors.

The irregular distribution is apparently determined by three factors, two of which can be guessed at and the third of which is unknown.

The association of the imbricated variety with the muddy cove can be accounted for best by natural selection. These flutings on the shell accumulate sediment. Although the shell may be white, it appears as mud-colored as the rocks on which the snail crawls. The fluting comes down, therefore, to a form of protective coloration.

The almost complete absence of the imbricated form from Somes Sound

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and adjacent waters can only be accounted for by assuming a change of sea level in recent times. The fiord topography of the Maine coast, with the drowned valleys of the rivers; the submerged channel of Union River, which enters the northern end of Blue Hill Bay and which can be followed on the chart under the sea for fifty miles beyond its present mouth; the presence of tree stumps in situ on the beach of Greening's Island, seven or eight feet below high-water line and fifteen feet below the level of present growing trees—all of these things indicate a very recent sinking of the sea bottom.

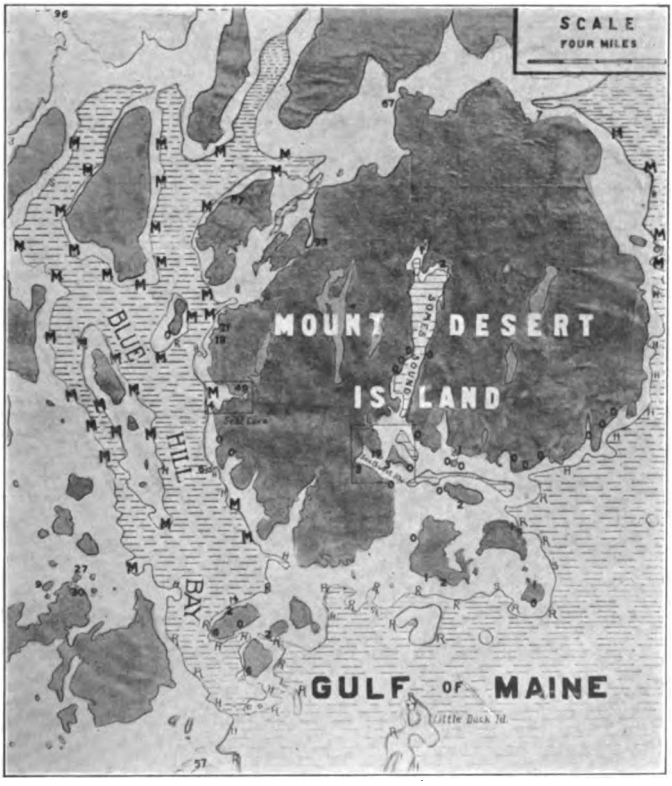


FIG. 6. A map of Mt. Desert Island, Maine, traced from a government chart. Cross-hatching shows the character of the coast line of Mt. Desert if the sea level were to fall 72 feet below its present position.

Character of the bottom at the 72 foot line: $M$ = mud bottom, $H$ = hard, $S$ = sand, $Sh$ = shell, $R$ = rocky.

The figures give the percentage of fluted shells at each station. The striking difference between the percentage in Blue Hill Bay and Somes Sound is well brought out.

If we assume that the sea once stood at a level 72 feet below the present low-water line, the map of Mt. Desert would be quite different than at present (see figure 6). To be sure, Blue Hill Bay would still wash its western shore, which would, as now, bear muddy coves, and Frenchman's

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Bay would wash the eastern margin; but the great indentation of the southern shore would not exist, and in its place would be rocky beaches, in some cases protected by a few low rocky islands, while a chain of three fresh-water lakes would lie in the present bed of Somes Sound.

If we study the present sea bottom, we find that no muddy coves could have existed on the south shore between Bass Harbor and Bar Harbor. The character of the bottom along the twelve-fathom line is shown in figure 6. If the same fauna occupied that region as now lives on the rocky southern shore of Mt. Desert, as the land sank and the sea water entered the chain of lakes it would carry with it a fauna without *imbricata*. The very few that are now found in this region and which are not associated with muddy coves could be accounted for by chance introduction by the birds that feed upon them. The 19 percent or 20 percent fluted found on the rocks of the South West Harbor steamboat wharf might have been introduced with the granite blocks which were transported in schooners from some of the upper bays during the construction of the wharf ten years ago. However, this is a mere guess. Be this as it may, the hypothesis of a change of sea level, which we know has occurred, will account for the almost total absence of *imbricata* from the shores of Somes Sound.

The fact that *Thais lapillus imbricata* appears on exposed situations on certain offshore islands (Little Duck Island 17 percent, Long Island 57 percent, and North Eddy Point on Grand Manan 95 percent) must be reserved for further study. It may be mentioned, however, that in exposed situations the imbricated forms are found only in fissures in the rocks.

## Conclusion

1. An examination of a large series of *Thais* (Purpura), the purple sea snail or dog welk, from one hundred and six stations seems to indicate that variations in size and shape of shells is the result of the direct effect of environment.

2. On the other hand, variations in color and shell sculpture are due to hereditary factors.

3. The proportion of any one color variety found at a single station is determined by natural selection. More light snails are found on light environments than on dark environments.

4. If two stations offering different backgrounds are near enough together so that snails can migrate from one to the other, the proportion of a color in one station will modify the proportion in another. In other words, if a dark environment is near a white environment, then more white snails will be found in this dark site than in another with no white habitat nearby.

5. On the shores of Blue Hill Bay the fluted *Thais* (Purpura auct.) *lapillus imbricata* is in general associated with mud flats.

6. In Somes Sound the fluted form is almost entirely absent and the few

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specimens that have been found are not associated necessarily with mud flats.

7. The present distribution of the imbricated form in Somes Sound can be explained by a recent change in sea level, a sinking of the land, carrying into the Somes Sound depression from the exposed coast a population free from *imbricata*. The few forms living there now can be explained as chance importations by birds and man which have not yet increased in sufficient numbers to occupy the region for which they are best adapted.

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# ON THE RELATION BETWEEN SPECIES AND AREA[1]

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In a recent article Arrhenius has attempted to reduce to a mathematical formula the general relation between the number of species and the size of the area.[2] This contribution was preceded by two others in which the same subject was discussed, neither of which I have been able to consult. Although the problem attracted the interest of some of the early phytogeographers, Arrhenius is, so far as I know, the first to develop an equation for the expression of his results. Since this equation appears to be wholly erroneous, a brief discussion of the question may not be out of place.

Arrhenius's work was done in the vicinity of Stockholm, where he made careful counts of the number of species in thirteen different and distinct associations. In every case he chose as a basis for his work, and as the unit area in his calculations, a quadrat of one square decimeter. For each association he examined a number of quadrats: 100 each in twelve associations and 300 in the other. For the former cases his quadrats were then combined by doubling into areas of 2, 4, 8, 16, 32, 64, and 100 square decimeters, and in the latter into areas of 1, 2 . . . 256, and 300 square decimeters. He does not say whether the quadrats as counted were contiguous or scattered. In every case he finds, as is already well known, that the larger areas contain the larger number of species, and this number is checked against the formula

$$\frac{\text{Area } 1}{\text{Area } 2} = \left(\frac{\text{Species } 1}{\text{Species } 2}\right)^n,$$

in which $n$ is stated to be a constant for each association. If this formula is correct, the number of species must increase continually as the area increases, and this conclusion is emphasized by him. The exponential ratio $n$ varies in the associations examined from 2.0 to 12.5, the higher ratios giving the lower rates of increase in species.

Let us first demonstrate the fallacy of Arrhenius's equation. He does not state the total size reached by any of the associations examined by him, but it is fair to presume that some of the woodland associations should certainly extend over an area of at least a square kilometer, which is equal to 100,000,000 square decimeters. In his "herb-*Pinus* wood," an average decimeter

[1] After this article was in type, a reprint was received of Du Reitz's contribution on the same subject, in Botaniska Notiser 1922: 17–36.

[2] Arrhenius, Olof, "Species and Area," Journ. Ecol. 9: 95–99. 1921.



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quadrat contains 4.8 species; a square meter contains an average of 33 species in fact and 41 in theory; the exponential ratio is 2. Substituting these values in his equation for a square kilometer, we have the equation

$$\frac{100}{100{,}000{,}000} = \left(\frac{33}{x}\right)^2.$$

Solving for $x$ we find that a square kilometer should contain the alarming total of 33,000 species. By the same formula, a single hectare of *Empetrum* moor should contain 319 species, while a square kilometer of "*Vaccinium vitis-Pinus* wood" should contain only between 9 and 10 species. In the first case the result is impossible; in the latter two it is incredible.

In my work on the structure of the plant association, statistics on the flora of the aspen association of northern Michigan have been secured, covering 240 quadrats of 1 square meter each.[2] This area contains a total of 27 species of vascular plants; a single quadrat averages 4.375, and the exponential ratio is therefore 3.01. The whole association, as developed in the immediate vicinity in one unbroken tract, covers not less than 25 square kilometers, and the total number of species according to Arrhenius' equation should be about 1,255. As a matter of fact, it is less than 100, and the total flora of the region, covering more than ten times this area and including numerous associations, is not known to equal the calculated flora of the one association.

A careful study of the distribution of species in any association brings to light certain interesting conditions affecting the general relation of species and area. Chief among these is the imperfection of associational uniformity. In every association certain species with high frequency index are uniformly distributed over the area. Species of low frequency may be uniformly distributed, but if they are of recent introduction into the area, or have poor means of dispersal, or are poorly adapted to the environment, they are often strongly localized. *If* the association were uniform, and *if* a quadrat were chosen of a size sufficient to provide the necessary space for the species, a single quadrat would contain the whole flora, and larger areas would, of course, show no increase in number of species. Such conditions of uniformity are never realized in nature, and a quadrat of such size is seldom chosen as a basis of investigation. Certainly it was not chosen by Arrhenius, who took a square decimeter as his unit.

If a smaller quadrat is chosen as the unit, each increase in size, by doubling the quadrats, will add some species until the area becomes large enough to include them all, and after that no increase will occur. The greater the uniformity of the association, the sooner will this limit be reached.

If each new set of quadrats examined is immediately contiguous to those of the preceding set, the resulting increase in species is different from that

[2] Gleason, H. A., "Some Applications of the Quadrat Method," Bull. Torrey Bot. Club 47: 21–34, 1920.

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obtained when the quadrats are all scattered throughout the whole area under investigation. This is due to the localization of many species, which may be completely absent from some sections of the area. In contiguous quadrats they may not appear at all, while in scattered quadrats there is a fair probability of some of them appearing early and of most of them appearing in any series of some size. The result in the former case is a relatively slow but long-continued increase in the flora as more quadrats are counted, while in the latter case there is a rapid initial rise followed by an early decline in the rate of increase. But in both cases the rate of increase shows a steady decline.

Arrhenius's error lies primarily in choosing quadrats of only a single square decimeter. Continuing them even to the number of 300 is not sufficient to reach a conspicuous reduction in the rate of increase of the species included; the exponential ratio remains practically the same, and he concluded that it would be maintained indefinitely. It is strange, however, that he has no inkling of what would happen on larger areas, since in 8 of the 13 associations examined his actual results for the maximum number of quadrats examined fell short of the expectation, and this shortage was the more evident the greater the number of species examined.

TABLE I. *Increase in number of species with increasing area, on contiguous quadrats as compared with scattered quadrats*

| Area in square meters | Contiguous quadrats | | Scattered quadrats | |
|---|---|---|---|---|
| | Species | Exponential ratio | Species | Exponential ratio |
| 1 | 4.375 | | 4.375 | |
| 2 | 5.817 | 2.43 | 6.667 | 1.64 |
| 3 | 6.900 | 2.37 | 8.750 | 1.49 |
| 4 | 7.600 | 2.98 | 10.367 | 1.70 |
| 5 | 8.208 | 2.90 | 11.292 | 2.61 |
| 6 | 8.950 | 2.16 | 12.650 | 1.61 |
| 8 | 9.667 | 3.73 | 13.800 | 3.30 |
| 10 | 10.333 | 3.35 | 14.875 | 2.98 |
| 12 | 11.250 | 2.14 | 16.250 | 2.06 |
| 15 | 12.250 | 2.62 | 16.938 | 5.36 |
| 16 | 12.000 | Negative | 16.667 | Negative |
| 20 | 12.917 | 3.04 | 17.667 | 3.83 |
| 24 | 13.500 | 4.12 | 19.400 | 1.81 |
| 30 | 15.125 | 1.96 | 20.000 | 7.34 |
| 40 | 16.167 | 4.34 | 20.333 | 17.36 |
| 60 | 19.750 | 2.14 | 22.750 | 6.42 |
| 80 | 20.000 | 23.13 | 22.667 | Negative |
| 120 | 23.50 | 2.51 | 25.000 | 2.77 |
| 240 | 27 | 4.99 | 27 | 8.99 |

The 240 quadrats of the Michigan aspen association have been given careful study in an attempt to discover whether or not the increase in species follows any regularity. In doing this they have been grouped into complexes of various sizes, and these complexes have been formed of both contiguous

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and scattered quadrats. Thus the group of ten contiguous quadrats has been formed of unit quadrats 1–10, 11–20, etc., while the group of ten scattered quadrats has been formed of units 1, 11, 21, . . . 231; 2, 12, 22, . . . 232, etc. The result is shown in Table 1.

In the contiguous quadrats it is seen that doubling the size causes a relatively slow increase in the flora, but this rate of increase is maintained fairly well throughout the series. In the scattered quadrats the rate of increase is at first more rapid, but is later retarded, until the two series are again equal when the whole area is regarded as a single quadrat. This is better illustrated by comparing the increase from 1 to 15 quadrats with that from 15 to 240 (Table 2).

TABLE 2. *Increase in number of species with increasing area*

| Area in square meters | Contiguous quadrats | | Scattered quadrats | |
|---|---|---|---|---|
| | Species | Exponential ratio | Species | Exponential ratio |
| 1 | 4.375 | | 4.375 | |
| 15 | 12.250 | 2.61 | 16.938 | 2.00 |
| 240 | 27 | 3.51 | 27 | 5.94 |

If these figures for scattered quadrats are plotted, using the areas as the abscissae and the number of species as ordinates, a somewhat irregular curve is obtained. When smoothed out free hand, it is seen to resemble the quadrant of an ellipse. If the ordinates of the smoothed curve are measured and the exponential ratios again calculated, a steady and gradual rise is discov-

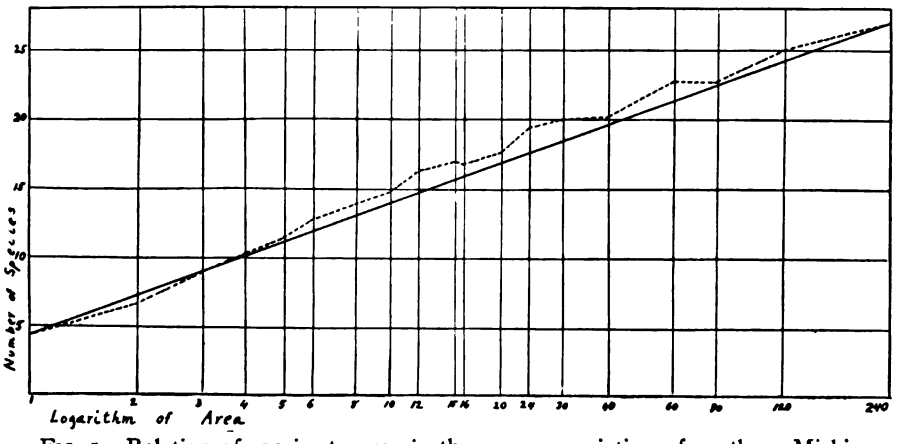


FIG. 1. Relation of species to area in the aspen association of northern Michigan. The horizontals indicate the area in square meters spaced according to the logarithm of the area. The verticals indicate the number of species. The dotted line indicates the number of species observed; the solid line indicates the number of species expected according to the logarithmic exponential equation.

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ered, indicating a progressive decrease in the rate of increase in the flora. The exponential ratio is therefore not a constant, as considered by Arrhenius. Over small areas, such as Arrhenius used, it may appear constant, but its variable character is revealed at once when larger areas of vegetation are examined.

Now, let another curve be plotted, as shown in figure 1, using as the abscissae not the areas proper, but the logarithm of the area, and using the number of species as the ordinates as before. The curve now approximates a straight line, and on this line the theoretical number of species per area may be read off directly. The greatest deviation between actual and theoretical numbers of species is found to exist at 24 quadrats, about 1.7 species or about 9 percent, whereas Arrhenius's formula produced much larger errors. In fact, the average deviation is only 0.87 species. A new exponential ratio may again be calculated in the original way and found to be 1.57. Applying this ratio to the whole area, estimated at 25,000,000 square meters, the total flora is calculated at 56 species. Since the counted quadrats were located only in the treeless portions of the association, and since several additional species are confined to the aspen thickets, this theoretical result corresponds closely with the known total of approximately 80 species. Similarly, new exponential ratios may be calculated for Arrhenius's plots. For the herb-*Pinus* wood the ratio is 1.22, for the *Empetrum* moor 1.13, and these figures indicate a total flora for one square kilometer of the former of 81 species, and for a hectare of the latter as 21 species. These figures are certainly much closer to the truth than those obtained by his original equation. The same results may also be obtained graphically.

It remains to be seen whether all plant associations exhibit a similar logarithmic relation of species to area. A large bulk of data collected for this and related statistical purposes by the writer was unfortunately lost, but the whole relation can be easily tested by any one so disposed.

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## REVIEW

### Methods for Expressing the Associations of Different Species

A recent publication on Malaria and Malarial Mosquitoes of the Far East[1] possesses much interest for ecologists on account of its containing a proposed "new method for studying the typical distribution of species," set forth on pages 7–24. This method is designed to show the relations of one species to others with which it is associated, and was devised by Dr. Hacker to illustrate the associations of Anophelines in the Malay States.

It consists (*a*) in adding to the number of times a species is found alone, the number of times it is found with each of the other species in a certain number of breeding places, this total being the number of "association units" available for that species; and (*b*) in expressing the component parts of this total as percentages; the percentage association of one species with each of the other species is termed its "association value."

Out of a number of illustrations of his method given by Dr. Hacker, we select the following:

*Anopheles hyrcanus* was found by itself 487 times, with *A. barbirostris* 169 times, with *A. vagus* 84 times, and with each of ten other species 78, 51, 46, 19, 16, 7, 5, 5, 3, 2 and 1 times respectively. The sum of these times is 973, which is the total number of association units. The association value of *A. hyrcanus* with *A. barbirostris* is 169 over 973 or 17.4 percent. (All the data used refer to the *larvae only* of these mosquitoes.)

Dr. Hacker's summary and conclusions are as follows:—

"(*a*) The method generally used for studying distribution is to collect descriptions of the breeding places of a species, in the hope that a description of the typical breeding place of that species may be evolved. Apart from the confusion that arises from the number of characters which require description, this method is defective, in the first place since it depends on personal impressions, and in the second place since these personal impressions are based on natural characters which vary from time to time. The method introduced in this volume is based on the number of times a given species is found with each of the other species in a certain number of breeding places. It is not based on personal impressions.

"(*b*) A peculiar merit of this method is that it enables past observa-

[1] Federated Malay States Malaria Bureau Reports. Vol. II. November, 1920. By H. P. Hacker, M.D., B.Sc. (Lond.) Medical Entomologist, Federated Malay States. Printed by Waterlow & Sons, Limited, London, Dunstable & Watford, 1921. 8vo., 47 pp., plans and diagrams. [The reviewer is indebted to the Editor of the Review of Applied Entomology, London, for his copy.]



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tions, of whatever dimensions, to be epitomised in a series of figures (the association values) showing the relative distributions of any given species.

"(*c*) This epitome can be used as a standard for estimating the probability of other species being found in company with any given species. When, therefore, any one species is found, it will be possible to prophesy what other species may be expected to be present in the same place. To prophesy with any degree of accuracy, the observations must be based on the widest experience, both in respect of number of observations and types of locality.

"(*d*) This epitome can also be used as a standard by which the distribution of any species can be measured in any area. The practical value of such a standard is that if the distribution in a newly investigated area does not conform to the standard, local causes must be sought for.

"(*e*) The epitome, however, merely reflects the past experience relating to the various species, and is much affected by the number of observations on each species. For example, on the few occasions a rare species is found. a certain species might always be present in its breeding place. Yet the association values of the common species would not show this close association merely because of the rarity of the associate; but the association values of the rare species would show the association.

"(*f*) The ideal way of overcoming this weakness would be to increase the data of the species with few records, until the basis of data for each species is of the same order of magnitude, but this is obviously impossible when rare species are being dealt with. At the present stage of the investigation the weakness may be overcome by taking into consideration the association values of both species in considering the relationship between them. Later, however, when the figures become adequate, a simple formula to express both sides of the relationship may be found.

"(*g*) In spite of the weakness of the method as a means for grouping the species into faunae, referred to in sections (*e*) and (*f*), the figures, even as they are expressed at the present stage of the investigation, show that the species may be grouped in [a certain] manner, and it is of interest to note that this grouping agrees closely with what is generally known about the breeding places of the species."

Prof. S. A. Forbes has called the reviewer's attention to a method which he devised in 1907[2] for determining what he styled the "coefficient of association" of any two species, the rule for which he stated as follows:

"Multiply the number [*a*] of collections made from the common area of the species by the number [*d*] containing one or more representatives of both; multiply the number [*b*] of collections containing one or more repre-

[2] On the Local Distribution of certain Illinois Fishes: an Essay in Statistical Ecology. Bull. Ill. State Lab. Nat. Hist. VII; article VIII. See also Journ. Ecol. III, pp. 12–13. 1915.

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sentatives of one of the species by the number [$c$] containing one or more of the other; and divide the first product [$ad$] by the second [$bc$]. The quotient will be the coefficient of association $\left[\frac{a\,d}{b\,c}\right]$."

On comparing these two methods it is evident that Dr. Hacker's does not consider the quantity $a$ of Prof. Forbes' where, being in the numerator and the largest quantity involved, it gives the coefficient a value of more than unity. The largest quantity (the sum of the number of times etc.) in Dr. Hacker's method is in the denominator, and the resulting association value is less than unity. It follows that in the latter method the association value is proportional to the number of times a given species (B) is associated with another species (C), a relation which does not hold in Prof. Forbes' formula. Prof. F. H. Safford, who has kindly looked into the mathematics of these two methods for the reviewer, calls attention to the facts that there is no relation between the coefficients of the two authors, and that neither method uses the number of individuals in the collections investigated. Dr. Hacker has appreciated the bearing of this omission, as is evidenced by his remarks under paragraphs $e$ and $f$ quoted above. He lays much stress on finding that most of the species studied by him have a larger association value each for itself than for any associated species, a condition which does not appear in Prof. Forbes' tables. Dr. Hacker's method involves fewer calculations than Prof. Forbes'. It will be interesting to test both of them by data derived from other groups of organisms.

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# PROCEEDINGS

## MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT TORONTO

### MEETING OF DECEMBER 28, 1921

### Preservation of Natural Conditions

The Committee on the Preservation of Natural Conditions, through its chairman, V. E. Shelford, presented the following report:

#### I. *General*

The Joint Chairmen plan has succeeded and should be continued. The National Research Council granted $300, which has provided for the publication of the report of the work of the committee as completed at the close of the Chicago Meeting, and has taken care of several other matters. The report will be sent to all members who apply in writing so long as the supply lasts.

#### II. *The List of Natural Areas*

The material has grown rapidly during the year. The greater part is in hand and the report, when completed, is likely to cover at least 300 pages. It will probably locate and briefly describe 1,000 areas. The matter on the U. S. National Forests, collected by C. F. Korstian, will be included.

The following work remains to be done:

1. Securing more information as to areas in a few states and in Canada.

2. The location of areas and collecting of information as to itineraries in Mexico and Tropical America. The Institute of Tropical Research will probably aid in this matter through securing information from official and other sources. The society is asked for permission to request that the American Society of Naturalists provide for a questionnaire to be sent to persons who have recently visited Mexican and South American areas, asking for information.

#### III. *Classification of Natural Areas*

The Classification of Natural Areas from the point of view of degree of modification is essential to the completion of such a list. Permission is requested to ask the American Society Zoologists to expend $25 on classification from the standpoint of animals, and the Botanical Society of America for a similar sum to classify from the standpoint of plants.

#### IV. *Name of List*

The name of the list is to be "A Naturalist's Guide to the Americas."



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### V. *State Organization*

Mr. Miller has been aiming to secure a committee member in each state. territory, and province who will attempt to stimulate the conservation of nature in his territory.

### VI. *Organization of Research Interests*

Dr. Sumner has sounded several organizations. One society voted to join a federation to conserve nature for research purposes. There is some interest in these matters.

### Recommendations

The Committee has voted to recommend the following:

1. That six joint chairmen be authorized.

2. That the present committee continue until July 1, 1922, and meanwhile undertake to complete the gathering of information.

3. That the completion and editing of the "Guide" be left to R. B. Miller, C. F. Korstian, V. E. Shelford, and one other person to be selected and approved by the Executive Committee. One person will be designated editor and be charged with securing publication facilities and editing the manuscript.

4. Standing or permanent Committee work:

*A.* Local Organization.

The Committee recommends that a chairman for local organization (in state, territorial, and provincial units) be selected to take the place of R. B. Miller beginning July 1, 1922.

The duties of this chairman to be:

*a.* To maintain a committee member in each state, province, and territory.

*b.* To maintain through the local representative a list of local societies interested in the conservation of nature and to request the appointment of a committee on the preservation of natural conditions in the local area (state, etc.).

*c.* To keep the society informed as to the conditions of natural areas through an annual report.

*B.* Organization of Research Interests.

The committee recommends that a chairman for "Organization of Research Interests" be elected to begin at the close of this meeting and serve until July 1, 1923, to take the place of F. B. Sumner, resigned.

5. The committee asks a grant of $60 for its work for the coming year.

6. The committee asks that it be authorized to request financial assistance of the National Research Council.

This report was accepted.

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## Pollution of Inland and Coastal Waters

The Committee on the Pollution of Inland and Coastal Waters, through its chairman, T. C. Nelson, presented the following report:

Owing to the rapidly growing menace of pollution of the streams and coastal waters of the country, the President of the Ecological Society appointed in April, 1921, a committee consisting of Professor C. A. Kofoid, of the University of California; Professor H. B. Ward, of the University of Illinois; Mr. F. C. Baker, of the Museum of Natural History of Illinois, and Professor T. C. Nelson, of Rutgers College, chairman, to consider the problem as it touches the field of ecology.

The present report is merely a statement of progress, hence the problem is barely outlined below. The first meeting of the committee was held in Toronto, December 30, 1921, with Professors Kofoid, Ward, and Nelson present. It was agreed at this meeting of the committee that the Ecological Society could best aid in the solution of the problem, not by urging drastic legislation to control pollution, but through fostering a campaign of education. Ecologists through their intimate contact with aquatic life see the effects of pollution vividly portrayed, and hence are in a position to warn the people of the country of the danger which confronts us all.

### The Problem of Pollution

#### I. *General Aspects of the Problem*

*A*. Destruction of fish and shellfish.

1. Most of the anadromous fishes which formerly ascended the streams of the Atlantic seaboard now no longer do so, since, first, the waters of these streams bear large quantities of factory and other wastes which render the waters distinctly toxic to fish life, and, second, the presence of these wastes has rendered the former spawning grounds unfit for this use.

2. The destructive effects of industrial effluents upon life in the coastal waters is very clearly illustrated in the case of the oyster in New England. During the past seven years, beginning with the outbreak of the Great War, and the resulting great industrial expansion, the oyster industry has been very materially reduced. To take the case of Rhode Island by way of example, rents from oyster lands have fallen from $136,000 to $50,000 per year, while the daily output of oysters has been reduced from 10,000 to 2,000 gallons. Throughout this same period, however, the industry in Delaware Bay, which as yet is not seriously affected by industrial wastes, has shown a steady increase.

*B*. The destruction of the biological machine of self-purification.

The association of bacteria, plants, and animals which aids so materially in the oxidation of putrescible wastes, and which plays so large a part in

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maintaining the purity of streams, is wholly or partly destroyed by industrial effluents, thus robbing the stream of its principal means of purification.

*C*. Spoiling of bathing beaches.

*D*. Destruction of boating and other forms of aquatic recreation.

This is due primarily to the unsavory nature of the water itself, and secondarily through the effect on fishing, which is one of the chief ends of aquatic recreation.

*E*. Despoiling of natural conditions.

Even minute quantities of foreign matter greatly modify the character and life of a stream; hence the ecologist who would study stream life in its primeval condition must now travel far to find a body of water which meets these conditions.

*F*. The disintegration of marine and fresh-water structures through the action of acid water.

*G*. The fire menace from floating oil.

While the last two aspects are primarily matters of engineering, yet it is a fact that these sides of the problem, together with that of the destruction of the biological balance, are the ones which are today engaging the most attention and are developing the most extensive research. An amendment to the Rivers and Harbors Act now before Congress provides a severe penalty for dumping overboard oil or oil wastes anywhere within the territorial limits of the United States or within 100 miles of shore.

## II. *Organizations Now at Work on the Problem*

1. The U. S. Public Health Service.
2. State and Municipal Boards of Health.
3. Municipal Sewerage Commissions.
4. U. S. Geological Survey.
5. State Geological Surveys and Natural History Surveys.
6. State Commissions of Conservation.
7. State Fish and Game Commissions.
8. State Boards of Shellfisheries.
9. U. S. Fisheries Bureau.
10. National Board of Fire Underwriters.
11. Individual investigators in the several universities and colleges of the country.

## III. *Situations to Be Met*

1. The throttling of industry as a result of strict enforcement of legislation forbidding the entrance of effluents to any bodies of water. Impossibility of enforcement of such legislation with our present lack of knowledge concerning proper means of waste disposal.

2. The inability of the layman to understand the problem involved. The need of a constructive nation-wide campaign of education.

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3. The thwarting of justice through the buying up of investigators by industries. This has already happened and is bound to occur many times in future unless scientific bodies take appropriate action.

4. Standards of pollution. What constitutes the danger line beyond which further pollution is unsafe; how are we to arrive at such standards: (*a*) conditions causing immediate death of the animals in the water, and (*b*) the much more difficult one to determine, namely, what constitutes the limit beyond which conditions become unfavorable for propagation of the species?

### IV. *The Problem for the Ecological Society*

1. To gather and render available all information on the effect of wastes and foreign materials on aquatic life.
2. To gather information as to ways in which problems of pollution have already been, in whole or in part, solved.
3. To keep individual investigators informed of the progress of investigations on the effects of pollution.
4. To foster a nation-wide campaign of education.
5. To aid eventually in framing constructive legislation.

This report was accepted and the committee ordered continued.

## Classification of the Content of Ecology

The Committee to Organize and Classify the Content of Ecology, through its chairman, W. G. Waterman, submitted a report which had been issued to the members in mimeographed form. There was some discussion of this report and the committee was instructed to further revise the outline submitted.

## Resolutions

The following resolutions, presented by Prof. L. H. Pammel, were unanimously passed:

### *On the Introduction of Non-native Plants and Animals in the National Parks*

Whereas one of the primary duties of the National Park Service is to pass on to future generations, unimpaired, the wilderness of the parks, including their native plants and animals; and

Whereas there are many educational and scientific reasons why the native plants and animals should remain unmixed through importations of other organisms not native to the parks; therefore be it

*Resolved,* That the introduction of non-native plants and animals in our National Parks be *strictly forbidden* by the park authorities, it being expressly intended that the planting of non-native trees, shrubs, and other plants, as well as the stocking of waters with fish not native to the region, is strongly opposed. Be it also

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*Resolved,* That copies of these resolutions be sent to Hon. Stephen T. Mather, Director of the National Park Service, to Mr. Horace M. Albright, Field Assistant to the Director, and to Mr. Robert Sterling Yard, Executive Secretary of the National Parks Association.

### *On Forestry*

WHEREAS the depletion of forest resources in the United States renders the development and application of sound forestry principles a matter of vital public concern.

WHEREAS the United States Forest Service is managing and developing the National Forests efficiently and in the best interests of the local communities and of the country as a whole, as well as furnishing leadership of inestimable value in forestry.

WHEREAS the work of the Forest Service is dependent upon that of the various branches of the Department of Agriculture.

WHEREAS the transfer of the Forest Service from the Department of Agriculture, by impairing the efficiency of the Forest Service, would jeopardize not only the forests, but the fish, game, wild life, and other resources dependent on the forests.

*Therefore be it resolved,* That the Ecological Society of America strongly favors the retention of the Forest Service and National Forests, including the Forests of Alaska, intact under the Department of Agriculture.

## MEETING OF DECEMBER 29, 1921

### SECRETARY-TREASURER'S REPORT

The report of the Secretary-Treasurer was submitted as follows:

*Meetings.*—The fifth annual meeting was held at Chicago during Convocation Week, 1920. A complete report of the business session of this meeting is given in ECOLOGY, 2: 155–160. At the sessions for the reading of papers the program was carried out in full. In addition, a summer meeting was held at Berkeley, California, under the auspices of the Pacific Division of the American Association. The Secretary wishes to acknowledge the valuable service to the Society of Prof. S. J. Holmes, who arranged the program and had charge of local details. By resolution passed at this meeting, the members of the Society resident in the territory of the Pacific Division have asked for the appointment or election, at the regular meeting of the Society, of an assistant secretary for this region, whose chief duty shall be the conduct of the meetings held under the auspices of the Pacific Division. The meeting for 1922 is to be held at Salt Lake City, according to present plans.

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*Membership.*—

| | | |
|---|---|---|
| Membership, Dec. 1, 1920 | | 458 |
| Resigned | 4 | |
| Deceased | 4 | |
| Losses | 8 | 8 |
| | | 450 |
| New members | | 104 |
| Total | | 554 |
| Paid for 1922 (Dec. 10, 1921) | | 267 |
| Not paid in advance (Dec. 10, '22) | | 287 |
| Total membership | | 554 |

| | | |
|---|---|---|
| Members in arrears more than | | |
| 2 years | 28 | |
| 2 " | 15 | |
| 1 year | 21 | |
| | 64 | 64 |
| Total paid up to Jan. 1, 1922 | | 490 |
| | | 554 |

*Financial Statement (Dec. 1, 1921).*—

*Receipts*

| | | |
|---|---|---|
| Balance from previous year (Dec. 1, 1920) | $195.88 | |
| Membership dues, including arrears | 1,504.17 | |
| Paid in advance for 1922 and 1923 [1] | 22.30 | |
| | $1,722.35 | $1,722.35 |

[1] This does not include dues for 1922 received in response to statements sent out Nov. 1.

*Disbursements*

| | | | |
|---|---|---|---|
| Printing—secretary's office | | $118.25 | |
| Ecology—regular quota | | 1,045.73 | |
| special appropriation | | 200.00 | |
| Postage, telegrams, messenger, express | | 65.74 | |
| Stenographer | | 25.60 | |
| Railway expenses of secretary (Chicago) | | 75.00 | |
| Committee on Natural Conditions | | 59.43 | |
| Pacific Division assessment | | 5.00 | |
| Membership Associated Mountaineering Clubs | | 15.00 | |
| Cash box | | 1.50 | |
| Exchange on Canadian checks | | 3.11 | |
| Checks returned | | 3.00 | |
| Advanced to Committee on Natural Conditions, to be charged against National Research Council Appropriation of $300.00 for the work of this committee. | | | |
| Clerical | $8.14 | | |
| Postage and stationery | 12.30 | | |
| Telegrams | 1.40 | | |
| | $21.84 | $21.84 | |
| | | $1,639.20 | 1,639.20 |
| Balance December 1, 1921 | | | $83.15 |
| Due from National Research Council | | | 21.84 |
| Balance | | | $104.99 |

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*Gifts.*—The Secretary has received, for the Society, copies of the following publications:

From the American Association for the Advancement of Science: Summarized Proceedings, etc., 1921.

From the Associated Mountaineering Clubs: A. F. Hall, Handbook of Yosemite National Park; L. R. Freeman, Down the Columbia; C. W. Beebe, The Edge of the Jungle; Arthur Heming, The Drama of the Forest; Vilhjalmur Stefannson, The Friendly Arctic.

It is desired that the Society make known its wishes in regard to the disposal of these and similar gifts.

Respectfully submitted,

A. O. Weese,
*Secretary-Treasurer*

This report was approved. The Secretary was directed to correspond with one of the geographical societies having headquarters in New York or Washington in regard to maintenance of a depository for books, etc., belonging to the Society. The choice of Secretary for the Pacific Division was left to the Executive Committee.

## Report of Business Manager of Ecology

The following report of the Business Manager of Ecology was presented and approved:

*Statement Showing Assets and Liabilities, December 1, 1920, to November, 1921*

*Assets*

| | | |
|---|---|---|
| Cash in hand | $468.35 | |
| Bills Receivable, Advertising | 80.00 | |

*Liabilities*

| | | |
|---|---|---|
| Bills Payable, New Era Printing Co., IInc., July issue [2] | | $357.77 |
| Assets over Liabilities | | 190.58 |
| | $548.35 | $548.35 |

*Circulation data as per Mailing List of October, 1921*

| | |
|---|---|
| 1. Members, Ecological Society of America | 460 |
| 2. Paid Subscribers | 258 |
| 3. Advertisers | 4 |
| 4. Exchanges | 21 |
| 5. Editorial Office | 12 |
| | 755 |

Number of copies ordered printed per issue 1000.

[2] Not including expense of Volume 2, number 4, which would change apparent "Assets over Liabilities" to a deficit.

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## Classification of the Content of Ecology

The Committee on Classification presented a revised report which was accepted as a provisional basis of classification and as a basis for discussion and ordered submitted for publication.

## Preservation of Natural Conditions

The Committee on the Preservation of Natural Conditions presented the following recommendations which were adopted by the Society:

Whereas the Society has approved a report calling for such action,

I. The committee nominates W. G. Waterman chairman for Local Organization to begin July 1, 1922.

The duties of this chairman are understood to be:

1. To maintain a committee member in each state, territory, and province of the United States and Canada in the manner in which such organization is already developed.

2. To maintain through the local representative a list of local societies interested in the conservation of nature, and to request the appointment of a committee on the preservation of natural conditions in at least one society in each state, province, or territory.

3. To keep the society informed of the condition of natural areas (especially changes) from year to year.

It is understood that the chairman will call for a report from the local representative each October 1 or thereabouts.

4. To maintain contact with the Research Information Bureau of the National Research Council.

II. The committee further nominates W. G. Van Name, of the American Museum of Natural History, chairman for National Organization to begin at the close of the meeting and serve to July 1, 1923.

The duties of this chairman are understood to be:

1. To interest national (and some local) research societies, universities, museums, and research institutes in the Preservation of Natural Areas (original flora and fauna) for research purposes, with a view to effecting a federation which can effectively approach legislatures or officials.

2. To represent the committee at the Intersociety Conference which is concerned with the federation of national societies.

The secretary of the Ecological Society is directed to request the National Research Council to include W. G. Van Name in the list of representatives.

3. To serve as delegate to the National Parks Conference to be held at the Palisades Park this spring.

III. It further nominates

F. C. Baker, of the University of Illinois Natural History Museum, to serve on the committee concerned with the publication of the "Naturalist's

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Guide," to be charged with circulating a questionnaire on the classification of areas and natural areas and itineraries in the tropics.

The matter of arranging for facilities for publication and putting the matter through the press to be carried out by either F. C. Baker or C. F. Korstian, as may be seen agreeable and expedient to them.

### Publication of Scattered or Local Contributions in Botany

The following communication from a committee of the Botanical Society of America was received, and the President directed to appoint a committee as requested:

*To the Systematic Section of the Botanical Society of America.*

*Gentlemen:* Your committee appointed at the meeting in Chicago on December 29, 1920, to prepare a resolution concerning means of publication for scattered or local contributions to botany (such as distribution and details of life histories), offers the following recommendation: That a committee of three be appointed from this section to confer with a committee from the Ecological Society and to suggest a plan of cooperative publication which would bring together fragmentary data which otherwise might be lost or less accessible. Further, that this committee consider means of encouraging and directing such work in order to bring attention to questions upon which information is desired, or to suggest investigations which may be combined to advantage.

(Signed) O. A. Stevens,
(Signed) John M. Coulter,
*Committee*

### Federation of Biological Societies

The following resolutions adopted by the conference called by the National Research Council Division of Biology and Agriculture to consider the Federation of Biological Societies were presented by the Secretary and were approved:

*Resolved,* (1) That it is the sense of this conference that an inter-society conference should be raised to study and report upon the feasibility of federation of the biological societies and to develop plans for the said federation.

(2) That for the purpose of effecting such an organization, each society and Sections F and G of the American Association for the Advancement of Science be requested to designate its president and secretary as member of an inter-society council which shall be authorized (1) to deal with all matters of common interest, such as pooling of programs, that are consistent with the existing regulations of the constituent societies; and (2) to draw up proposals for a constitution and by-laws of a federation of the societies in question and to present them for action at the next annual meeting.

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## National Research Council's Committee on the Atmosphere and Man

The following resolution was passed:

The Ecological Society of America views with great interest the work of the National Research Council's Committee on the Atmosphere and Man. It heartily endorses the report adopted by the committee October 22, 1921. It specifically approves of the general statement of the plan of the studies of the atmosphere and man in the general science of ecology. It also approves the projects which are now being taken up as outlined in the plans appended to the report; and it especially urges the value and the necessity of establishing an institution for ecological research along the lines laid down by the committee.

## Election of Officers for 1922

A nominating committee composed of Henry C. Cowles, Charles C. Adams, and Z. P. Metcalf proposed the following for office:

For President, Forrest Shreve, Tucson, Arizona; for Vice-President, Henry E. Crampton, New York; for Secretary-Treasurer, A. O. Weese, Champaign, Illinois. There being no other nominations, the candidates were unanimously elected.

The meeting was adjourned.

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# ZOOLOGICAL ABSTRACTS

**Alexander, C. P.** The crane-flies of New York. Part II. Biology and Phylogeny. *Cornell Univ. Agri. Exp. Sta.* Memoir **38**: 704–1129. 1920. An extensive contribution to the general biology of the Tipulidae containing many data of ecological bearing. P. S. WELCH.

**Arey, L. B.**, and **W. J. Crozier.** Natural history of Onchidium. *J. Exper. Zool.*, **32**: 443–502. 1921. *Onchidium floridanum* Dall is a nudibranch mollusk that lives in crevices in rocks situated in the between-tide zone on ocean beaches. Colonies of about a dozen live in a single crevice. Each individual leaves the crevice to feed for about an hour during each twenty-four hours. After feeding it returns to its "home" crevice and will not remain in any other crevice. Homing is due to contact-odor stimulation, and there is no evidence of associative memory. A. S. PEARSE.

**Barney, R. L.**, and **B. J. Anson.** Relation of certain aquatic plants to oxygen supply and to capacity of small ponds to support the top-minnow (*Gambusia affinis*). *Trans. Amer. Fish. Soc.*, **1920**: 268–278. 1921. The authors found that submerged vegetation increased the dissolved oxygen content of ponds, while a mat of surface vegetation greatly decreased the oxygen supply, each case being compared with that of a pond having no visible vegetation. In a similar set of artificial ponds, the Gambusia production was found to be increased in ponds with submerged vegetation and decreased in those covered with surface vegetation. The influence of other factors was unfortunately not determined, the effect of the vegetation on the food of the fish being alone considered, and not in a convincing manner. C. L. HUBBS.

**Bergtold, W. H.** The English Sparrow (*Passer domesticus*) and the motor vehicle. *Auk*, **38**: 244–250. 1921. The author finds a decrease in the number of English Sparrows in the city of Denver, due to the introduction of motor vehicles in traffic, and the displacement of the horse, upon whose fecal droppings the sparrow chiefly subsists. T. C. STEPHENS.

**Cole, A. E.** Oxygen supply of certain animals living in water containing no dissolved oxygen. *Journ. Exp. Zool.*, **33**: 293–320. 1921. An attempt to solve the oxygen problem of animals living at the bottom of certain inland lakes during the summer stagnation period. Attention is devoted mainly to the larvae of *Chironomus tentans*. An oxidizing substance, possibly atomic oxygen, may form the necessary oxygen supply. P. S. WELCH.

**Gross, Alfred O.** The Dickcissel (*Spiza americana*) of the Illinois prairies. *Auk*, **38**: 1–26, 163–184. 1921. This paper includes data from a census survey in Illinois, showing distribution by crop habitats, and in latitudinal portions of the state. As to food the author found that immature Dickcissels, whose adult food has been found to be largely animal matter (insects), consisted largely of vegetable matter (seeds), and explains this on the basis of lack of skill and adeptness of the young birds. The author estimates that the more than a million Dickcissels of Illinois consume 100,000,000 insects per day, which means the saving of $4,680.00 worth of hay daily. T. C. STEPHENS.

**Hecht, Selig.** The photochemistry of the sensitivity of animals to light. *Science*, n. s., **53**: 347–352. 1921. A general summing up of the work done on the photosensory activities of animals by the author up to the time the article was written is given (*Journ. Gen. Physiol.*, **1**: 147–166, 545–558, 657–666, 667–685; **2**: 299–246, 337–347, 499–



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517, and *Proc. Nat. Acad. Sci.*, **6**: 112–115). It has been shown: (1) when exposed to light, *Ciona intestinalis* and *Mya arenaria* respond only after a measurable interval, which is usually longer than one and a half seconds; (2) the animals will respond to light only of increased intensity; (3) after a response the same intensity fails to produce any additional effect; (4) the animal when placed in the dark very soon recovers its sensitivity to light. The action of light, in its photosensory effect, depends on intensity and time. If intensity alone is varied, the effect is proportional to the logarithm of the intensity. If time alone is varied, the effect is proportional to the time. When both the intensity and time are varied, the photochemical effect is equal to the product of their separate activities: $V = kt \log I$. E. B. POWERS.

**Juday, Chancey.** Observations on the larvae of *Corethra punctipennis* Say. *Biol. Bull.*, **40**: 271–286. 1921. Relation of the larvae of *Corethra punctipennis* to the biological complex of Lake Mendota and certain neighboring lakes. Quantitative data for both deep and shallow water extend over the entire year. Gravimetric and chemical results are included. A distinct contribution to the problem of biological productivity. P. S. WELCH.

**Nelson, Edward W.** Lower California and its natural resources. *Mem. Natl. Acad. Sci.*, **16**: No. 1. 194 pp., 34 pls. 1921. In Lower California five natural faunal areas are recognized: San Pedro Martir, San Diegan, Colorado Desert, Vizcaino Desert, and Cape. These subordinate faunal districts are partly independent of the distribution of the life-zones, of which Arid Tropical, Upper Sonoran, Lower Sonoran, and Transition are recognized; an infusion of Canadian species is found on the higher mountains. Lists are given of the characteristic birds, mammals, and plants. Detailed descriptions are given of physiography and vegetation. L. R. DICE.

**Powers, Edwin B.** The variation of the condition of sea-water, especially the hydrogen-ion concentration, and its relation to marine organisms. *Publ. Puget Sound Biol. Sta.*, **2**: 369–385. 1920. Powers deals with the variations in pH and dissolved oxygen in Puget Sound. He found the relation of these factors to one another and to the hydrographic features of the region to be very complex, owing to the strong currents of the region. In the vegetation along shore the pH and oxygen content are subject to larger and more rapid fluctuations than in open water. C. L. HUBBS.

**Powers, Edwin B.** Experiments and observations on the behavior of marine fishes toward the hydrogen-ion concentration of the sea-water in relation to their migratory movements and habitat. *Publ. Puget Sound Biol. Sta.*, **3**: 1–22. 1921. The author finds that "the fishes which live on the bottom and among vegetation," "in definite habitats irrespective of the pH of the water," "did not react to a gradient of hydrogen-ion concentration," and he concludes that such fishes "select their habitats by factors other than the hydrogen-ion concentration of the water." The three free-swimming species studied reacted quickly and specifically to the pH gradient, and "were always found in water having a pH at or near that to which they reacted positively in the experiment." Powers concluded that the hydrogen-ion concentration or $CO_2$ tension of the water is a factor in the habitat selection and migration of such types. The investigation was admirably executed, and the report is supplemented by remarks on the physiological factors involved, and by a useful bibliography. C. L. HUBBS.

**Richardson, R. E.** The small bottom and shore fauna of the middle and lower Illinois River and its connecting lakes, Chillicothe to Grafton; its valuation; its source of food supply; and its relation to the fishery. *Bull. Ill. Nat. Hist. Surv.*, **13**: 363–554, 1 chart, 9 maps. 1921. This is an admirable quantitative study of the fauna and productiveness of a river. The bottom animals, chiefly mollusks, are most abundant where there is least current and most mud. The plankton passing Havana is about

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200,000 tons (wet) per year, or 20 to 50 times the total dry weight of the flesh of the bottom animals in the 138 miles above the mouth of the river. The total wet weight of bottom animals (without mollusk shells) in different miles varied from 10.4 to 5,196 pounds per acre. Analyses show that the nitrogen content of the bottom sediments is many hundred times that of the flesh of animals living in them. A. S. PEARSE.

**Sumner, Francis B.** Desert and lava-dwelling mice, and the problem of protective coloration in mammals. *Journ. Mammalogy*, **2**: 75–86, pl. 6. 1921. Fifty specimens of canyon mouse (*Peromyscus crinitus stephensi*) from an isolated field of very dark lava rock in the Mojave Desert are not appreciably different in coloration, as determined by the tint photometer, from an equal number of specimens from a region of pale colored rocks in the same desert. As the species is restricted to rocky places the colony on the lava field must have been isolated by the surrounding sand for a long period of time. Its failure to change in color to approach that of its dark substratum throws doubt on the explanation of protective coloration, derived through the action of natural selection, applied to local color races of mammals, especially those which occur on lava fields. L. R. DICE.

**Swarth, H. S.** Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. *Univ. Calif. Publ. Zool.*, **21**: 75–224. 1920. A remarkably careful and painstaking systematic analysis of one genus of birds, the Fox Sparrows. The very precise determination of the distribution of the various geographical races recognized in the one species of this genus, together with the great range in climatic and biotic variation in their habitats, makes an inquiry into the relation between the two germane. The author offers some observations upon this subject, and concludes that humidity in the breeding area is not the cause of melanistic tendency; but, "taking the whole year through, it is evident that the darkest colored forms (*annectens, townsendi,* and *fuliginosa*) are under more or less humid conditions continuously, and during the winter months under an extreme of such exposure. Of the paler colored races (*unalaschcensis, insularis,* and *sinuosa*), one at least (*sinuosa*) nests in a region of extremely heavy precipitation, and the others where fogs and cloudy weather prevail much of the time, but they all spend the winter, a longer period than the nesting season, in an arid portion of the country" (p. 95). A further analysis of physical factors is brought to bear upon the facts of migratory movement of the various geographical races of this group. Studies of this kind go far to justify the recognition and designation of subspecies, which otherwise have little meaning. T. C. STEPHENS.

**Ward, Henry B.** Some features in the migration of the sockeye salmon and their practical significance. *Trans. Amer. Fish. Soc.*, **1920**: 387–426. 1921. In this paper as elsewhere, Dr. Ward has with much justice criticized the vagueness of most theories which have been proposed to explain the anadromous spawning migrations of salmonoid fishes. He has made an effort to determine the physical factors responsible for the movements of one of these fishes, the sockeye salmon, in fresh water. While the general method of attack seems both sound and promising, the reviewer is of the opinion that the data obtained by the author (he considered only temperature in detail) is yet too meager to justify the drawing of extensive conclusions, particularly as, in the present case, the conclusions seem rather discordant with the large volume of critical data obtained by Gilbert and others on the general life history and migration of these fishes. C. L. HUBBS.

**Wilson, C. B.** Dragonflies and damselflies in relation to pondfish culture, with a list of those found near Fairport, Iowa. *Bull. Bur. Fish.*, **36**: 185–264, 3 pls., 63 figs. 1920. An ecological consideration of the relation of odonate nymphs and adults to pond culture of food fishes. Food relations receive special attention. P. S. WELCH.

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Collaborators for Zoological Abstracts and their subjects are as follows:

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A. G. Ruthven—Reptiles; Amphibians.
Frank Smith—Annelida; Fresh-water sponges.
T. C. Stephens—Birds.
P. S. Welch—Aquatic insects.

Authors publishing papers of general ecological interest will confer a favor by sending reprints to the proper collaborator. If in doubt the paper may be sent to Lee R. Dice, University of Michigan, who will see that it reaches the proper person. It is especially desirable to have attention called to papers published elsewhere than in the usual zoological periodicals.

## NOTES AND COMMENT

### Summer Meeting for 1922

The 1922 Summer Meeting of the Ecological Society of America will be held in affiliation with the American Association for the Advancement of Science at Salt Lake City, Utah, June 22 to 24, inclusive. In addition to an independent meeting, the Ecological Society will meet jointly with the Western Society of Naturalists. A series of field trips in the interesting region surrounding Salt Lake City is being planned by the local committee. The program is in charge of Dr. A. G. Vestal, Stanford University, California, Western Secretary, to whom titles of papers should be sent as soon as possible.

### Field Meetings

During the first years of the organization of the Ecological Society one of its prominent activities was the organization of ecological field trips, particularly during the summer. One such trip was conducted this year, with great success, in connection with the meeting at Tucson, Arizona, of the Southwestern Division of the American Association. Other similar trips are planned in connection with the Salt Lake City meeting. The Secretary will be glad to assist in the organization of, and give due publicity to additional excursions to be held under the direction of members of the Society.

### Weir Mitchell Station of Harpswell Laboratory

The Weir Mitchell Station of the Harpswell Laboratory, which was established on Mt. Desert Island, Maine, last summer (Ecology 2: 234, 1921), will open for research on June 25. The non-toxic salt water supply is being installed, and will be ready at that time.

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ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

OFFICIAL PUBLICATION OF THE

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VOLUME III, No. 3 JULY, 1922

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ESTABLISHED, 1920

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Edited for the British Ecological Society

By A. G. TANSLEY

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CHANGES IN THE COAST VEGETATION NEAR BERROW, SOMERSET. By H. STUART THOMPSON. (With Map and Plate II.)

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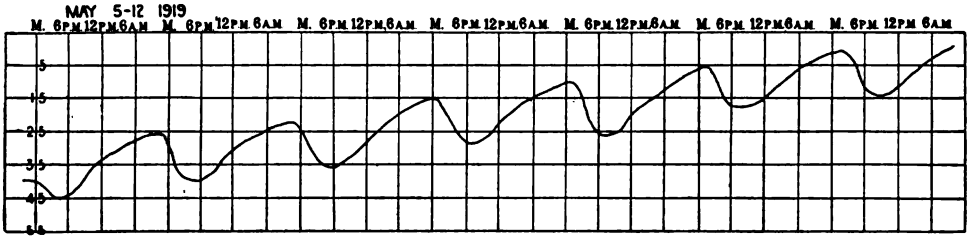


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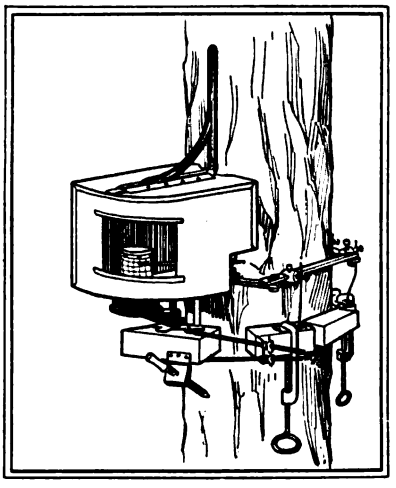

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[See "**Growth in Trees,**" Publication 307, Carnegie Institution of Washington, 1921]

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# ECOLOGY

VOL. III JULY, 1922 No. 3

## THE PROBABLE EFFECT OF THE CLIMATE OF THE RUSSIAN FAR EAST ON HUMAN LIFE AND ACTIVITY

STANISLAUS NOVAKOVSKY

*Clark University, Worcester, Massachusetts*

If, as in the Arabian fairy-tales, it were possible to bring the past before our eyes again so that we could follow the first steps of human civilization, then we could, without doubt, see how great has been the influence of geographical conditions. We should see how nature determined the first and most difficult steps of humanity, sometimes giving human beings numerous opportunities and opening wide and easy paths to progress, and again without pity keeping whole nations during long, long centuries without the least ray of light.

From the material on hand, which has been gathered by students of geography, ethnography, history, and other branches of science, we must conclude that all of mankind's customs and inclinations, its physical characteristics, and the anthropological types of various nationalities, as well as the very germs of its religious beliefs, are due first of all, and above all, not to some unseen, supreme power, but to the law-abiding forces of nature. If we could sum up all the present knowledge about nature, it would be possible to conclude without hesitation that the surrounding nature has always had a deep and irresistible influence on all the branches of the vegetable and animal kingdom, as well as on the physical and spiritual nature of man. Geography recounts the history of geographical conditions, and among them the chief place of importance belongs to the climate. On it depends the material as well as the spiritual organization of governments, and on it is based all their future.

Explorers in Siberia have constantly noted the influence of the climate on its life. Of these observations, the most notable are those of the famous Russian scientist, Prof. A. Midendorff. In his work, "Travels to Northern and Southern Siberia," Part I (St. Petersburg, 1860), which constitutes an epoch-making event in the study of Siberia, he says: "Nowhere in all the world does the climate act in such an unfriendly manner toward vegetable and animal life, not excluding man, as it does in Siberia. Nowhere but there

[**Ecology**, Vol. III., No. 2 (pp. 89–180) was issued May 18, 1922.]



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is the character of the country preconditioned to such minute details by the climate, and nowhere is the triumph of life over the enmity of the outside world so complete as in Siberia." The very distinguished and not less famous scientist, G. N. Potanin,[1] also says: "The chief factor is nature, which preconditions the physiognomy of a country and its landscape, the fauna, and even the civilization of man. The peculiarities of the Siberian climate will, without fail, affect the art of the country likewise, if art ever appears on Siberian soil. In painting, one may suppose that Siberia will produce good colorists. And in music, also, the influence of nature will undoubtedly be powerful." This opinion, more optimistic than Midendorff's, is at best true only of western Siberia, rather than of the Russian Far East. In general, we may say that the chief error of many Russian as well as foreign scientists lies in the fact that they draw their conclusions for all Siberia as a whole, whereas it possesses many marked differences and peculiarities. It is as impossible to characterize the climate of Siberia as a whole as it would be to characterize the climate of the United States or Europe.

Many articles, pamphlets, and even books have been written about the climate of Siberia and that of various sections of Siberia, but no one has undertaken to draw the parallel between the climatic and the cultural peculiarities of this part of the Asiatic continent. Nor is there such a work for the Russian Far East, which, generally speaking, has been studied very little. It is astonishing to see how the climate of the Russian Far East has been neglected by scientists as well as by the government. Here are two very characteristic examples. In 1891 the Amur region was visited by the well-known Russian scientist and botanist, Prof. S. Korginsky, with the special intention of acquainting himself with the condition of agriculture. As the result of his investigations, there appeared in the Bulletin of the Eastern Siberian Branch of the Russian Geographical Society for 1892 a very interesting account of his expedition. But among many valuable and interesting facts which he brought out no space was devoted to the climate. The administration, as well as the scientist, had almost entirely forgotten this very important factor. Another explorer, toward the end of the nineties of the last century, while studying Sakhalin, asked a very responsible member of the administration about the climate of Sakhalin and received the following reply: "The climate of Sakhalin? Well, this is such a dirty place that it has no climate."

It would be incorrect to conclude from these instances that the Russian Far East has been entirely untouched by investigations. In a number of works sufficient respect is paid to the climate of this territory. First among them should be mentioned the works of such men as Professor Woeikov, Dr. N. Kirilov, Prof. K. Bogdanovich, Doctor Slunin, Professor Schmidt, Professor Komarov, Mr. F. Schperk, and Mr. Yuvachev. But all the works of all these men were only first attempts, and they fall far short of giving a

[1] Potanin, G. N. Nudzhi Siberin (Needs of Siberia) p. 265, St. Petersburg, 1908.

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complete picture of this exceedingly interesting part of Russian Asia. We shall try, in this article, to draw a parallel between the conditions of the climate and the living conditions of the population.

We shall begin our analysis on the most important basis of all—the economic basis. In studying the climate of the Russian Far East, one notices without difficulty that, thanks to local peculiarities, the country is subdivided into several regions.[1] In our work we have distinguished the following several regions: (1) Chukotsk-Anadyr, (2) Kamchatka, (3) Okhotsk, (4) Sakhalin, (5) Nikolaevsk, (6) Ussuri, (7) Amur. These are subdivided into still smaller sub-regions. We may characterize briefly all of these regions according to their chief economic features in the following table:

TABLE I. *Regions of the Russian Far East and their economic features*

| Region | Possible extent of agriculture | Principal branches of present economic life | Other branches of economic life capable of development in near future |
|---|---|---|---|
| Chukotsk-Anadyr .. | Impossible | Hunting, fisheries, reindeer-breeding | Mining |
| Kamchatka..... | Almost impossible | Hunting, fisheries | Forestry, animal-breeding, vegetable-raising |
| Okhotsk..... | Impossible | Hunting | Animal and reindeer-breeding to a certain extent, vegetable-raising |
| Nikolaevsk..... | Possible to a certain extent | Fisheries | Animal-breeding, agriculture, mining |
| Sakhalin..... | Possible to a limited extent | Fisheries, agriculture, mining | Forestry, agriculture to a limited extent |
| Ussuri..... | Possible to a wide extent | Agriculture, fisheries, mining, forestry | Manufacturing |
| Amur..... | Possible to a wide extent | Agriculture, hunting, fisheries, mining, forestry | Manufacturing |

Even from this brief table one can see clearly that the economic regions depend definitely upon the climatic conditions. The greatest attention, certainly, should be given to agriculture, as it is the basis of the nation's welfare and progress. It would be very interesting and important in this respect to establish the limits within which agriculture flourishes, or, in other words, the

[1] These regions have been described by the writer in "Climatic Provinces of the Russian Far East in Relation to Human Actvities," Geographical Review, Vol. 12, No. 1, pp. 100–115, 1922.

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limits within which barley is raised, as that is the grain which is grown farthest north. The well-known meteorologist, Wild, found, for example, that the northern limit of barley culture coincides with the isotherm 5° C. in May. But this restricts the limits too much and is not justified by the facts. Prof. A. Midendorff, in establishing the northern limit of barley culture according to historical and economical evidences, in the area between the rivers Obi and Lena, gave it as 61–62° N. latitude, and added that the Okhotsk mountain range brings it farther south, extending it into the Amur Province. But in the present state of our knowledge of Siberia such a limit can not be established. In any case, however, whether the limit extends farther north or farther south, the main determining cause will always be the climate. And finally it may be concluded unmistakably that the climatic peculiarities, such as the temperature, humidity, winds, fogs, etc., of the Okhotsk, Kamchatka, and Chukotsk-Anadyr regions, exclude all possibility of the development of agriculture in these regions. Consequently this vast part of the Russian Far East is entirely useless for agricultural colonization, and the population may be increased, therefore, only by the development of other industries, chiefly fisheries. In other regions, however, particularly Ussuri and Amur, where the climate has an entirely different aspect and possesses milder and more favorable features, agriculture exists and in the future may reach a considerable degree of development. Even here, though, we find that not all the parts of these regions are favorable for agriculture, and this difference is due not so much to the various kinds of soils as to the climatic peculiarities.

Here we must repeat and emphasize especially the fact that many unfavorable features which appear as a result of the climate may in the future be avoided. Agriculture, so to speak, is the arena wherein man struggles with nature, overcoming its inertia, its avarice, its defects, and its obstacles. Thus, struggling and overcoming, the agriculturist tries with the given natural conditions to increase and broaden the productivity of the land. By such a struggle the future population of the Russian Far East will be able to avoid many of the unfavorable conditions caused by the climate. In 1899, for example, the Ussuri Railroad was finished. Before the laying of this line the region between the rivers Ussuri and Lefu was rendered so swampy by the humid climate during the period of the summer rains that there was no communication whatever. As a result of the laying of the railroad, this vast area with its splendid fertile soil, which had before been desolate and almost unpopulated, has changed character entirely. Flocks of cattle and cultivated fields of grain appeared soon after the railroad came; there were thousands of haystacks to be seen, and the population became denser. Village after village sprang up in places where before there were only swamps and forests. Communication became easier, and gradually the obstacles which were created by the climate were removed.

Fish takes the place of bread in the Russian Far East. Consequently,

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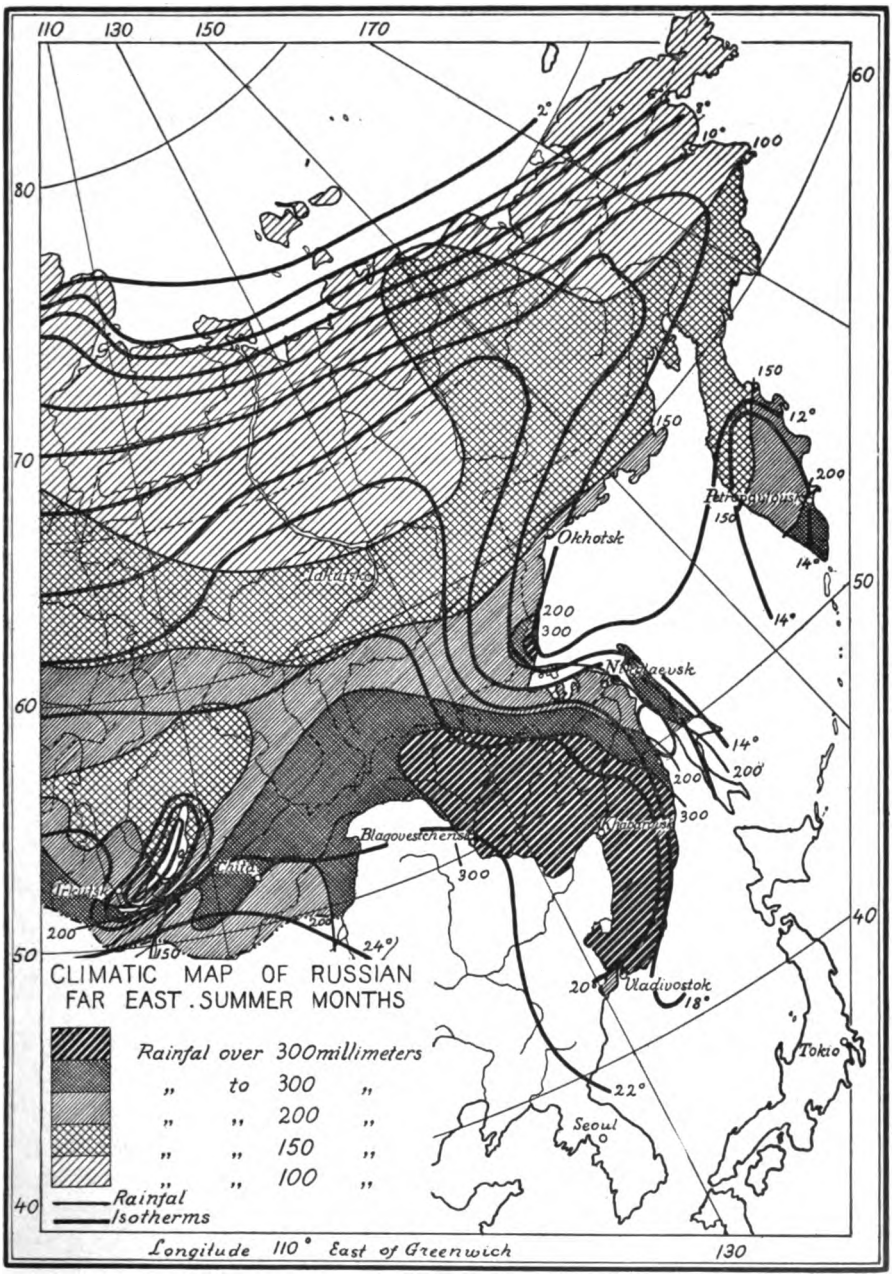


FIG. 1. Summer temperature and precipitation of the Russian Far East.

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fishing plays a very important part among the activities of the population, and in some sections it is the chief occupation. A scarcity of fish is of as great importance in the northeastern parts of the Russian Far East as a bad harvest of grain is in other sections. A fish famine brings the same sorrowful and disastrous consequences as a bread famine in Europe. The climate plays as important a part in the fish industry as it does in agriculture, being either a benefactor or a merciless enemy. The most serious climatic element in this respect appears to be the dampness and the large number of cloudy days. The lack of salt, the primitive methods of salting and preparing the fish, compel the fishers in almost all of the northeastern part of the Russian Far East, namely, the Okhotsk, Kamchatka, and Chukotsk-Anadyr regions, to dry the fish by the natural heat of the sun. As the drying of the fish takes place chiefly in the second half of July and August, the number of rainy and cloudy days during that period is of great significance. While the fog in some places, as in London, for instance, deprives many people of pleasure and perhaps has some slight effect on the stock exchange and the retail trade, in far northeastern Siberia it means life or death for many hundreds of people, and may bring about fatal consequences to the entire country. The following table contains the number of cloudy and rainy days for the fishing season in the chief fishing localities:

TABLE II. *Cloudy and rainy days of summer in the chief fishing localities*

| Station | Cloudy and partly cloudy days | | | | Rainy days | | | |
|---|---|---|---|---|---|---|---|---|
| | June | July | Aug. | Total | June | July | Aug. | Total |
| Okhotsk | 23 | 28 | 31 | 82 | 21 | 24 | 13 | 58 |
| Petropavlovsk | 19 | 28 | 30 | 77 | 15 | 27 | 27 | 69 |
| Nikolaevsk | 29 | 29 | 26 | 84 | 5 | 9 | 12 | 26 |
| Nikolskoye | 21 | 24 | 21 | 66 | 3 | 7 | 3 | 13 |
| Nayakhan | 30 | 24 | 21 | 75 | 11 | 19 | 15 | 43 |

In other words, in all this part of the Russian Far East, where the fish supply is so important, the largest part of the summer is characterized by cloudy days, which are very unfavorable for the preparation of fish. But nature, as if compensating for its severity, sends cold weather early, and thus provides the primitive method of freezing to prepare or to complete the preparation of the fish, which is consumed in this region not only by man, but also by his faithful companions, the team dogs. There are other factors which also considerably injure the fishing industry and serve as very influential climatic obstacles in this branch of the national activity. These include the long winter period; the freezing of the harbors, the shores, and the estuaries of the rivers, and the lateness of the period when they are freed

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from ice in the spring; the autumn cold spells; the heavy fogs of the spring and autumn; and the strong winds.

The climate is not less influential in the matter of cattle and stock breeding. The chief and almost the sole occupation of the country of the Chukchi, commonly called Reindeer Chukchi, is reindeer breeding, which proves so profitable that the people do not take time to hunt or to fish. Consequently, for part of the population of the Russian Far East, this occupation plays the predominating rôle. The reindeer provides food, clothing, and the means of communication, and is therefore the main supporter of life. But even the reindeer, which might seem to be able to stand all the mischief of the climate of the extreme north, nevertheless suffers from it at times. The severe and snowy winters affect the reindeer very injuriously, because the moss tundras become hidden under the snow, which makes it difficult to secure food. In the summer the reindeer have plenty of food, but if the summer is especially hot, they suffer from the gad-fly, the abundant growth of which is favored by the tundra. Many of the diseases of the reindeer, too, are found to be in close connection with the climate. A general murrain among the reindeer, or a poor catch of fish, or a spoilage of the fish, will cause many of the aboriginal tribes of the Russian Far East distress which can not be imagined. Finally, the dogs which are so important in the life of the extreme north frequently perish from the fish famine or from the contagious diseases, which, although their cause is not exactly known, seem to be connected with the climatic conditions of the country.

Cattle breeding is also greatly affected by the climate. The low state of its development in the Amur Province at present is due to the following peculiarities: the heavy summer rains; the lack of nourishing herbs, caused by the excessive moisture and lack of sunshine; the lack of good pastures; and the abundance of noxious insects. In the future, with the development of agriculture and the increase in the planting of root crops, there will probably be a considerable increase in cattle breeding, and many of the unfavorable influences of the climate will be overcome.

In the Maritime Province the climate is milder, the vegetation more abundant, and the pasture period longer. The winter, however, is long and cold; but there is good mowing, and in general there are better climatic conditions for the development of cattle breeding. Furthermore, noxious insects are absent from this section, thanks to the oceanic winds, which drive them inland. In the rest of the region, although cattle breeding is possible, the climate is so severe as to hinder its development. This is true also of the Okhotsk and Kamchatka regions.

Hunting also constitutes a very important occupation in the Russian Far East, as well as in Siberia. Many of the aboriginals as well as the Russians pursue it daily. The climate influences hunting, as well as the other occupations, directly and indirectly. The indirect influence is due to the fact that

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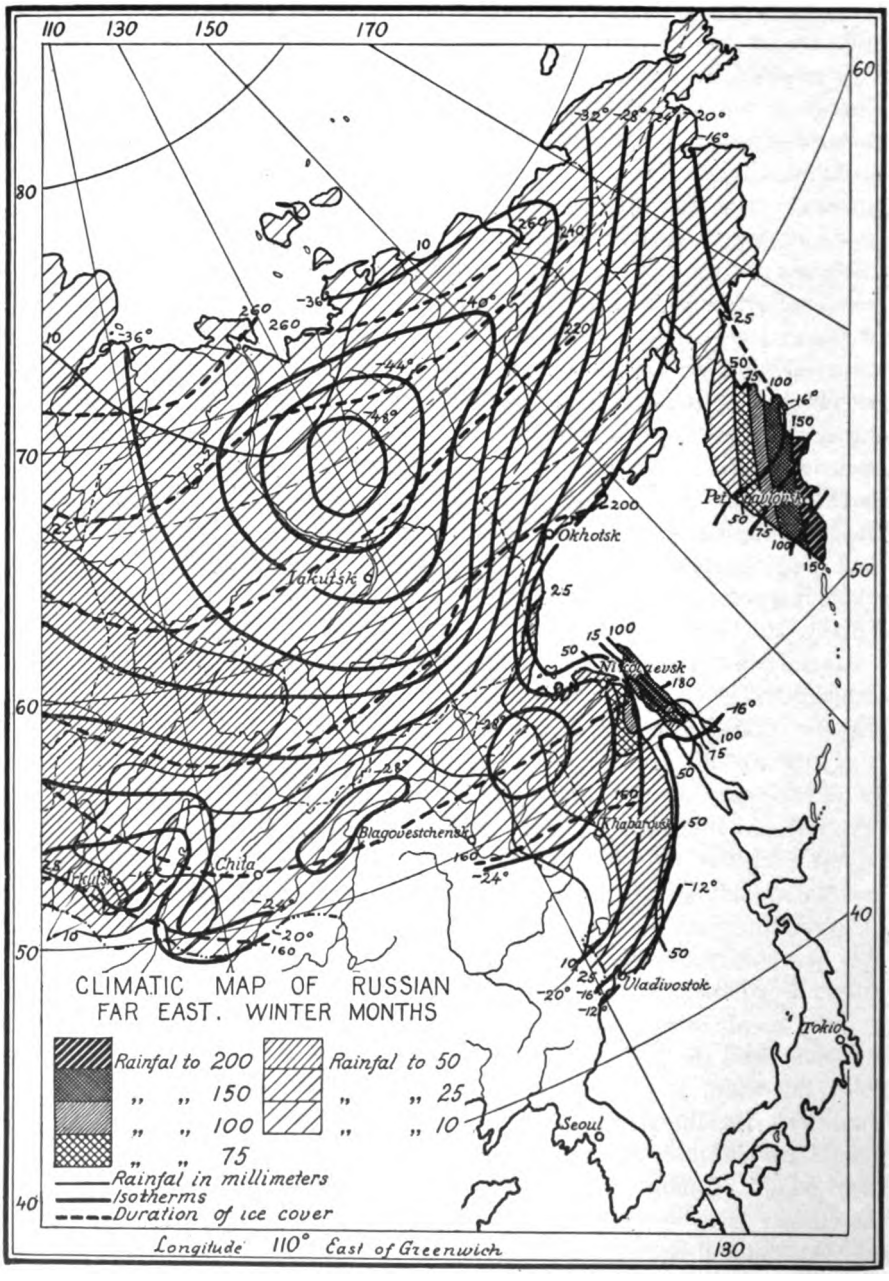


FIG. 2. Winter temperature and precipitation of the Russian Far East.

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the climate, as was shown previously, determines the character of the forests and their limits of spreading, preconditions an abundance or lack of food for many animals, and determines also the very character of the forest animals. The direct influence shows itself in the species of the animals as well as in the nature of their fur, which is the greatest attraction and the chief object of the hunting. Besides the more or less severe winter, the lack or the abundance of snow, the formation of the crust of ice, the sleet, the thawing, the distribution of the rainy days, the storms, etc., all affect the migration of the animals, as well as the course of the hunting. Thus the climate either favors the hunter or deprives him of his chief support. The sleet and the icy crust which frequently destroy many animals are particularly unfavorable.

We have seen by this time that all of the chief branches of the economic life are in close dependence on the climate. Although its influence is felt by the settlers as well as by the native population, it is more powerfully exerted on the aboriginals, who remain in a very low state of civilization. They are mere playthings in the hands of nature and are helpless to struggle with its surprises.

Let us turn now to the general question of population and its density. The statistical data for the conditions in the Russian Far East are as follows:

TABLE III. *Population of the Russian Far East and its density*

*Kamchatka Province*

| Districts | Total | Population per verst (0.66 sq. mi.) |
|---|---|---|
| Petropavlovsk | 11,900 | 0.04 |
| Anadyr | 11,000 | 0.02 |
| Ghizhighinsk | 8,500 | 0.05 |
| Commandore | 1,700 | 1.1 |
| Okhotsk | 5,500 | 0.03 |
| Chukotsk | 1,900 | 0.04 |
| Total | 40,500 | 0.21 |

*Maritime Province*

| Districts | Total | Population per verst (0.66 sq. mi) |
|---|---|---|
| Khabarovsk | 99,000 | 0.4 |
| Yman | 124,300 | 2.4 |
| Nikolsk-Ussuriisk | 195,800 | 2.9 |
| Olginsk | 49,800 | 1.0 |
| Ussuriisk Cossacs | 137,700 | 1.6 |
| Total | 606,600 | 1.7 |
| Amur Province | 250,400 | 0.7 |
| Sakhalin Province | 33,500 | 0.3 |
| Total Russian Far East | 931,000 | 0.9 |

It will be noticed that these statistics have been given according to political divisions, which agree only in part with our climatic divisions.

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The total population of the Russian Far East, therefore, amounts to only 931,000 souls. The density is very small. For the sake of comparison, let us say that the density of the population of European Russia is 28 persons per square verst; the density for all Russia is 8.7; the density for Siberia, 0.8; and in the Russian Far East it is only 0.9. In the territory now under discussion, as may be seen from Table III, the densest population is found in the south of the Maritime Province, the Zeya-Bureya plain. Such a distribution of population is in complete accordance with the conditions of climate. Moreover, this region offers the most favorable conditions for agricultural activities.

The races which make up the population vary widely among themselves, as will be made clear in the following table:

TABLE IV. *Population by races*

| Race | Amur, percent | Maritime, Kamchatka, and Sakhalin, percent |
|---|---|---|
| Russians | 86.8 | 52.6 |
| Turco-Tatars | 8.2 | 1.4 |
| Poles | 1.0 | 1.9 |
| Finns | 1.0 | 0.3 |
| Jews | 0.9 | 0.7 |
| Lithuanians | 0.3 | 0.2 |
| Germans | 0.2 | 0.4 |
| Mountaineers (Caucasians) | 0.1 | 0.1 |
| Armenians | — | 0.1 |
| Mongolians | — | 23.0 |
| Miscellaneous | 1.5 | 19.3 |

The aborigines of the territory consist of many tribes, which are very unevenly distributed. These people predominate in the northern parts, while in the southern sections their percentage is insignificant. The extreme northern district, that of Anadyr, and the extreme southern, Ussuri, are widely different in this respect. While in the former these tribes constitute about all of the population, 88.4 percent, in the latter they are almost entirely absent, the percentage being only 0.4 percent.

The aborigines of the Maritime Province and Kamchatka are composed of the following racial groups:

| | |
|---|---|
| Palaeasiatics | 25,401 |
| Tungus | 18,649 |
| Yakuts | 466 |
| Mongolians | 164 |
| Total | 44,680 |

By the name Palaeasiatics should be understood several ancient aboriginal tribes inhabiting the northeastern and some of the remote eastern districts of the Russian Far East. In their physical type and language, as well as in

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their customs, they stand quite alone among all the aborigines of Siberia. The tribes with their numerical strength may be indicated as in the following table, the data being those of the year 1903:

| Tribe | Men | Women | Total |
|---|---|---|---|
| Aleuts | 287 | 284 | 571 |
| Ainus | 7 | 7 | 14 |
| Gilyaks | 1,420 | 1,225 | 2,645 |
| Kamchadals | 1,316 | 1,291 | 2,607 |
| Koryaks | 3,830 | 3,701 | 7,531 |
| Chukchis | 5,061 | 5,154 | 10,215 |
| Eskimos | 631 | 676 | 1,307 |
| Yukagirs | 42 | 48 | 90 |
| Chuvantsi | 222 | 199 | 421 |
| Total | 12,816 | 12,585 | 25,401 |

The Aleuts are found only on the Commodore Islands; the Gilyaks in the Uda district; the Chuvantsi, Yukagirs, and Eskimos in the Anadyr region; the Kamchdals in Kamchatka; the Chukchis in the Anadyr region and the Ghizhiga district. The Koryaks are scattered in different parts of the Okhotsk, Kamckatsk, and Anadyr districts. With the exception of the Chukchis, none of the above-mentioned tribes is increasing in number; in fact, some of them are gradually disappearing. The Kamchadals, Yukagirs, and Chuvantsi are nearly all Russianized; the Aleuts have partly adopted Russian customs; the Gilyaks, Chukchis, Eskimos, and wandering Koryaks have best preserved their national peculiarities. The Tungus tribes of Kamchatka and the Maritime Province consist of the following:

| Tribe | Men | Women | Total |
|---|---|---|---|
| Goldi | 2,638 | 2,376 | 5,014 |
| Oroches | 1,329 | 1,078 | 2,407 |
| Neghidalians | 232 | 191 | 423 |
| Samagirs | 210 | 215 | 425 |
| Manchurians | 21 | 1 | 22 |
| Soloni | 7 | 8 | 15 |
| Olchi | 700 | 795 | 1,495 |
| Tungus and Lamuts | 4,544 | 4,304 | 8,848 |
| Total | 9,681 | 8,968 | 18,649 |

Some of the Tungus tribes have a half-settled mode of life and some are nomads. Each tribe, however, has its own region. Thus the Tungus tribes are scattered in small numbers in the Amur region, particularly along the Amur River and its tributaries, and in the unreached and unexplored northern and eastern parts.

Besides the natives and the Russian immigrants, the population of the Russian Far East is composed of Coreans, Chinese, and Japanese, who are present in great numbers.

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The Russian part of the population of the eastern borderland is composed exclusively of immigrants at present. The first attempts to populate the Amur and Maritime provinces were made in 1858. At first, however, as a result of the long distances, lack of railroads, and slackness on the part of the government in taking steps toward furthering colonization, these attempts met with little success, and up to 1883 only 9,000 people had arrived. Practically speaking, the colonization of the country did not begin until the eighties, when the government changed its views on the colonization question radically and took steps to encourage immigration. Systematic help was organized to aid the immigrants in settling the country. The development in immigration during a period of fifteen years is shown by half decades in the following table:

| | 1896–1900 | 1901–1905 | 1905–1910 | 1896–1910 |
|---|---|---|---|---|
| Amur Province | 14,755 | 12,841 | 67,739 | 95,333 |
| Maritime | 6,476 | 16,081 | 133,561 | 156,118 |
| Total | 21,231 | 28,922 | 201,300 | 251,453 |

The following figures show the average yearly immigration for the period from 1909–1913 in each of the provinces:

| | Men | Women | Total |
|---|---|---|---|
| Amur Province | 11,772 | 3,306 | 15,028 |
| Maritime Province | 11,423 | 3,748 | 15,171 |
| Sakhalin | 4 | 0 | 4 |
| Kamchatka | 2 | 3 | 5 |
| Total | 23,151 | 7,057 | 30,208 |

In 1914 the migration movement to the East increased so much that, in spite of the war, the total number of peasants who migrated from European Russia to the land beyond the Ural Mountains reached 336,409, which was 8,979 more than in 1913.

Immigrants to the Russian Far East are contributed mostly by the Ukraine, which contains the provinces of Poltava, Volynia, and Podolia. From the data of the Russian Statistical Committee it can be deduced that in the Amur Province, Ukrainians constitute about 40 percent of the white population, and in the Maritime Province the proportion is still higher.

The high percentage of emigrants from the southwestern provinces leads to the following very interesting fact, which is connected with the climatic conditions of the Russian Far East. In spite of the fact that up to the Russian Revolution in 1917 the Russian Far East was being more and more

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occupied by settlers, there was observable at the same time a reversal of the current of migration, namely, a movement back to the native provinces of European Russia. The unsuitable natural conditions were probably the chief cause of this. According to the estimates of the author's colleague in the University of Kiev, Professor T. Yamzin, 45.4 percent of the settlers from the Maritime Province and 39.5 percent from the Amur Province returned home for these reasons. If we should consider indirect causes and influences, the percentage would be considerably increased. Among the natural conditions the climate occupied the first place. The reason for this is the character of the climate of the localities from which the settlers came. The peasant coming from the southwestern provinces of European Russia to the Russian Far East and finding an entirely different course of climate, after a short struggle with the new conditions, gives up everything, takes his possessions, and returns to his sunny home.

Among the population of the Far East, as in the case of the inhabitants of European Russia, a large percentage is occupied with farming. The last census, 1897, shows that in the Amur district 67,956 persons of both sexes were engaged in agriculture. This constitutes 56.5 percent of the population, which is divided according to nationalities in the following manner:

| | Population | Agriculturists | Percentage |
|---|---|---|---|
| Great Russians | 82,373 | 41,514 | 50.4 |
| Ukrainians | 21,096 | 18,508 | 87.7 |
| Tungus | 1,350 | 350 | 26.3 |
| Manchurians | 3,344 | 2,202 | 65.9 |
| Chinese | 7,816 | 3,695 | 47.3 |
| Koreans | 1,552 | 1,243 | 80.1 |

In the Maritime and Kamchatka provinces the agricultural population is distributed by districts as follows:

| | Population | Agriculturists | Percentage |
|---|---|---|---|
| Khabarovsk | 27,288 | 1,082 | 4.0 |
| Ghizhighinsk | 7,492 | 5 | 0.1 |
| Anadyr | 12,084 | ..... | 0.0 |
| Commandore | 651 | ..... | 0.0 |
| Okhotsk | 4,732 | ..... | 0.0 |
| Petropavlovsk | 8,365 | ..... | 0.0 |
| Udsk | 18,232 | 1,366 | 7.5 |
| South Ussuri | 124,830 | 61,027 | 48.9 |
| North Ussuri | 19,662 | 9,645 | 49.1 |

From this table it can be seen that almost the entire agricultural population is centered in that region which is called Ussuri. As to the nationalities which participate in agricultural pursuits in the two districts, the following data can be given:

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| | Total | Farmers | Percentage of farmers |
|---|---|---|---|
| Great Russians | 80,178 | 19,359 | 24.1 |
| Ukrainians | 33,326 | 28,359 | 85.4 |
| Poles | 3,198 | 60 | 1.9 |
| Hebrews | 1,571 | 9 | 0.6 |
| Tatars | 1,034 | 24 | 2.0 |
| Tungus | 16,967 | 1,191 | 7.0 |
| Chukchi | 10,237 | ..... | 0.0 |
| Koryaks | 6,058 | 4 | 0.1 |
| Kamchadals | 3,978 | ..... | 0.0 |
| Eskimos | 1,099 | ..... | 0.0 |
| Gilyaks | 4,213 | 8 | 0.2 |
| Chinese | 30,904 | 3,992 | 12.9 |
| Coreans | 24,306 | 19,834 | 81.6 |
| Japanese | 2,094 | 33 | 1.6 |

It follows that the Russian population is chiefly occupied with agriculture and the aboriginal population with hunting, fishing, and the breeding of the reindeer. Moreover, while the Russian population is all settled, most of the aboriginals lead a nomadic kind of life. This condition is accounted for by the fact that some aboriginal tribes, at first under the pressure of the Mongol tribes, and later of the Russian newcomers, were obliged to move constantly to the places where the newcomers would trouble them the least. In these places the climate was not suited to agriculture, and they were obliged to choose either fishing or hunting, or, as a last resort, reindeer breeding. The Chukchi and Koryaks pass the winter in the interior of the country, where their reindeer find more food, and in the summer they move to the sea-shores, where noxious insects do not trouble the animals.

Some of the aboriginal tribes populating the Russian Far East have been partly assimilated, others are rapidly disappearing, while still others succeed in preserving their native customs and even increasing their numbers. The cause for this should be sought in the economic conditions, moral and political. Not being able to adapt themselves to the conditions which have been created by the incoming elements, the aboriginals suffer greatly, and with each year they decrease in number. As examples, we may cite the Chuvantsi and the Yukagirs. The only tribe which is increasing is the Chukchi. They have also preserved the best of their primitive peculiarities. This condition is undoubtedly closely connected with the climate. At first glance this will seem paradoxical, as nowhere is the climate so severe as in the territory inhabited by the Chukchi. It was the law of self-preservation, rather than desperation, which drove them to settle in this unfavorable corner. Coming here under the influence of some unknown historical cause, probably to escape oppression by some other people, they created for themselves by the severe climate a fortress inaccessible to communication and conquest, more stable than the primitive arrows or ditches, and stronger than the bullets of the modern gun. For a very long time the Chukchi were unconquerable. And even the present

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representatives of the Chukchi, although they are considered to belong to the Russian domain, remain in fact absolutely independent, on account of their inaccessibility. Japan owes to the mildness of her climate the energy of her population, and to her island location is due her independence; but to an even greater degree do the Chukchi owe their existence, growth, and long preservation of their tribal originality to the climate.

The chief occupation of the Chukchi is reindeer breeding, and consequently their food is almost exclusively reindeer meat. But the Chukchi, like all other people, need vegetables. Where are these to be obtained, then, if they can not grow in the climate of this extreme northeast? In the summer the Chukchi eat the sprouts of many plants, mixing them with reindeer blood, and in winter, as a substitute for vegetable food, they extract the half-digested moss from the stomach of the reindeer and prepare a mash-like green substance of a disagreeable odor, color, and taste. This is called "monyals" (in the local language, "pilkapil"). Some of the Chukchi are very fond of this strange dish, but in most cases it is prepared only in times of need.

Even the religious beliefs of the people in the Russian Far East are connected with the climate. Rocks and trees, mountains and clouds, the elements of wind, rain, thunder, etc., are supposed to be living creatures. All these things, animate and inanimate, may be enemies or friends of man, hence the need to obtain the good disposition of the most powerful, to consider them as good gods, and to insure for themselves their defense against others, the evil gods. Here may be found the beginnings of primitive religion, in the creation of which a large part is played by the climatic conditions, the influence of which, whether injurious or beneficial, is very evident in the case of the primitive population.

Now we shall pass to the very important question of the relation of the climate to the health of the population. Here, for the time being, we shall limit ourselves to only a general discussion, based chiefly on the observations of explorers and inhabitants, and in another paper we shall summarize the whole matter with statistical data. The long and severely cold winter is common to the largest part of the Russian Far East. The winter cold, according to the conclusions of Professor Ellsworth Huntington, which are based upon extensive data, is the most trying element in the climate of the northern United States. It is also the one whose effect can most easily be mitigated, however, provided proper attention is paid not only to temperature, but to atmospheric moisture within doors. This is certainly an undeniable truth, especially if the cold increases and decreases gradually, without sharp jumps or drops; if the winter weather is clear and calm; and if the air is pure and sufficiently humid. In this respect Amur is probably the most healthful region, as all these conditions prevail during the winter; and the least healthful, perhaps, is the Okhotsk region, because of the excess of cloudiness and winds. In the northern parts of the Russian Far East the prolonged dark-

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ness, as well as the low temperature, appear to make the winters extremely trying. The summers are also not equally healthful everywhere. The great number of fogs and the exceeding cloudiness along the coast probably cause depression, and thus affect the physical condition and energy of man. Besides, it has been noticed in the Amur and Maritime provinces that the hot days decrease the appetite, the digestion is weakened and disordered, and the skin perspires very much and becomes withered. From a sanitary standpoint, the hot and humid climate influences the growth of different micro-organisms, which often get into the drink and food and cause diseases of the intestinal system, which are particularly injurious to children. The autumn of the Amur and Maritime provinces is warm, calm, and moderately humid, without fogs or frequent rains, and must therefore be considered the most healthful season. In general, considering all the climatic elements, the most healthful locality appears to be the southern sub-region of the Ussuri region, which belongs to the Maritime Province.

Of the diseases observed by physicians, the most frequent are those of the lungs, which have generally the nature of colds. It would be erroneous, however, to ascribe these to the climate. As a matter of fact, we find low temperature accompanied by winds everywhere during the winter. Local habits and conditions of living have much to do with the health conditions. In the houses it is unbearably warm, and the air is extremely dry, and thereby diseases of the respiratory organs, as well as other diseases, are promoted. Moreover, the inhabitants must often come outdoors for various purposes. The difference between the temperature of the yard and that of the houses often exceeds 50° C. Such a condition naturally leads to the contraction of colds. This is proved, furthermore, by the fact that colds are frequent among the settlers and very rare among the natives. The clothing of the settlers is often not in accordance with the needs of the season, and the food during the winter is not sufficient for the greater part of the population. That is why the number of diseases and deaths increases in the winter. In Verkhoyansk, for example, seven tenths of the deaths of the entire year occur during the winter. In some parts of Siberia there are also very frequent cases of malaria, but in the northern and eastern parts of the Russian Far East fever is almost unknown, and in others it is very rare. This fact is in close relation with summer temperature. It has long been considered that the mean isotherm of 60° F. (15.5° C.) in the Northern Hemisphere is the boundary of endemic malaria, and it has also been found that for the development of malarial infection this mean temperature is necessary over at least 16 days. In the northern part of the Russian Far East malaria is unknown because this temperature of 60° F. never lasts over 16 days. This is also explained by the fact that on the Okhotsk shore in Kamchatka and in the Chukotsk-Anadyr region the vegetation is not so rich and in some places is very scanty, offering no shelter to mosquitoes and other insects. The chief form of vege-

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tation, the tundra, freezes, and there are consequently no conditions favorable to the development of fever. In the Maritime Province, too, in spite of the abundance of mosquitoes and favorable temperature for development of malarial infection, malaria is almost unknown because of the deep freezing of the soil, which kills the pests.

Next in frequency are the diseases of the stomach, which are common in summer, particularly in the Amur and Maritime provinces, and especially among children. This disease is caused by the food, which must often be eaten unripe. The difference between the temperatures of the day and the night also affect the stomach and the intestinal parts. In the northern and northeastern portions of the Russian Far East also stomach diseases are frequent, but they occur mostly in the winter time. In these sections this form of disease is found to be in direct connection with the condition of the food and its methods of preparation. The trouble begins with the use of the fat animal food, which is badly salted and insufficiently dried. As a result of eating it, there develop a catarrh of the stomach and special kinds of stomach sores, as well as inflammation of the peritoneum and other disorganizations of the digestive system. It should be added, however, that the climate preconditions the kind of food and the methods of its preparation, and the climate must therefore be considered the indirect cause of these diseases. Rheumatism is found everywhere in the Russian Far East. In the eastern parts it appears as the result of the cold and humidity, common in winter, autumn, and spring. In other localities it seems to result from local conditions—the agricultural activities of the autumn, winter, and spring, and the hunting and fishing. Diseases of the eyes are very frequent in the north and northeast. They seem to be due chiefly to two causes. The first is the blinding white snow cover, which is particularly irritating in the spring, when the sun shines on it brightly. The aborigines use hand-made spectacles as a protection against the snow, but they are so badly made that they offer almost no help at all. The other cause is the smoke that abounds in the house, in connection with the usual uncleanliness of household life. The climate, therefore, influences these diseases only indirectly. But whatever the causes, they are so serious that at times they bring about the entire loss of sight. They are spread so rapidly that the physicians are often helpless to give any medical assistance. Moreover, the diseases entail very serious consequences to the population in general, because in the case of the illness of the head of a family, he is not able to earn a living for those dependent on him, and this leads frequently to the perishing of the whole family.

Psychic and nervous disorders occupy a prominent place among the diseases of the Okhotsk-Kamchatka region. They are often marked by very peculiar phenomena. The first symptom appears to be a severe headache, from which the patient suffers exceedingly. When a man is afflicted with such disorders, he may run into the forest, or jump wildly over the tundra,

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or even climb the mountains. Not finding peace of mind, he frequently attempts suicide. Often the patient screams and howls, talks nonsense, throws and breaks things, and sometimes faints. Hysterical diseases are very common in the Okhotsk region, as a rule, and at times acquire an epidemic character. Doctor Slunin tells us that he often observed such cases. In a quiet company of people one member would begin to scream, others would take it up, and soon the whole house would be filled with cries and screams. Those affected suffer cramps and convulsions and undergo fainting spells, and soon the floor is a mass of crawling, distracted creatures. Cases of insanity are also common, particularly among the newcomers.

We do not know the exact connection or relation between these diseases and the climate, but the writer thinks that the cause lies in the monotony of the long winter, the absence of bright sunny days, and the general disposition toward depression which these conditions bring about. All of these conditions undoubtedly influence the minds of the people, depressing them and inducing nervous disorders. Women are more subject to such diseases than are men, because they have more impressionable natures, and are more subject to their surroundings.

In the Yakutsk Province leprosy is found in a very distressing form, causing panic and fright among the aborigines. This disease is also found in Okhotsk and Kamchatka, and occasionally in other regions. It has probably very little connection with the climate, because it is found in all climates and on all soils. Scurvy was quite widely spread throughout the Russian Far East some time ago, but, as in the case of leprosy, the connection between the disease and the climate is very slight. Influenza, however, is a very frequent disease, and, according to Professor Huntington, is undoubtedly connected with the climate. It affects aborigines, even, especially in the extreme northeastern parts. Of other diseases, such as typhus, measles, syphilis, etc., we shall not speak here, for they show, at least in the Russian Far East, less connection with the climate than with the social and economic conditions.

The study of the climate in relation to the health of the population is a very complex matter and presents many problems which are hardly capable of being solved. The meteorological records are not sufficiently long and continuous, and the statistical material in regard to the diseases and mortality are not exact. This lack of sufficient data is felt particularly in the case of the aborigines, because no class of people is closer to nature, more completely in its power, and suffers more severely from its destructive influences than do those who remain in the most primitive state of civilization. For this reason, we have given only a general account of the health conditions of the Russian Far East, basing our statements solely on the observations and experiences of explorers and inhabitants.

Unfortunately there is no exact statistical data at my disposal relating to the mortality in the Russian Far East by months, but the following table can serve as an excellent illustration of Yakutsk Province:

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| | | | | | |
|---|---|---|---|---|---|
| January | 665 | persons | July | 345 | persons |
| February | 610 | " | August | 229 | " |
| March | 1,049 | " | September | 359 | " |
| April | 578 | " | October | 417 | " |
| May | 485 | " | November | 454 | " |
| June | 822 | " | December | 499 | " |

From the above table we can see that the highest mortality is in March and June, constituting almost 29 percent of the total number of deaths which occurred during the entire year. In the rest of the months the percentage of mortality gradually decreases and reaches its minimum in August. This fully confirms all of our conclusions mentioned above.

The striking number of deaths for June can be explained by the fact that in the summer time there is observed in the Russian Far East, in Yakutsk Province, and in general all through Siberia, a considerable mortality amongst children which is due to an epidemic of intestinal diseases, to which children are particularly susceptible. And in general the number of deaths is the largest among children up to one year, as, for instance, in Yakutsk Province in 1890, nineteen percent of the entire number of deaths was that of children at the age of one year.

The influence of the climate on health might best be illustrated by giving statistics on the death rate compared with the variability and present conditions of the climate. But such a comparison is impossible with the data which we now have. We are limited, therefore, once again to general information. The statistics on the death rate are as follows:

| | Births per 1000 persons | Deaths per 1000 persons | Natural growth of population |
|---|---|---|---|
| European Russia | 48 | 34 | 13 |
| Amur and Maritime provinces | 50–60 | 25–30 | 25–30 |

It appears, then, that the mortality in the Russian Far East is less than that in European Russia. But it is probable that the figures given above are too small, especially for the tundra of the Russian Far East, where no authentic census has ever been taken. If we consider that sanitary and hygienic conditions in the Russian Far East are worse than can be imagined in England and America, and that conditions are particularly bad among the settlers, then we shall have to attribute the low mortality to the healthfulness of the climate. The mortality is especially high in the case of children. Of 100 deaths in the Amur Province, 74 occur among children below the age of five. In the Ussuri region the mortality among children of the same age amounts to 66. Two causes may be assigned to this: (1) the poor sanitary and hygienic conditions, which affect children especially severely; and (2) the variability of the climate. The mortality is probably also due to some extent to direct climatic influences. One other fact should be noted in this

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connection, namely, that together with the great mortality among children, a very high death rate is also observed at other ages in the case of newcomers. For example, among the native inhabitants the death rate per 1,000 inhabitants is only 22, while among the settlers the number reaches 31. Such a condition is to be attributed not so much to the climate itself as to the marked change in moving from one climate to another. The new settlers, not being acquainted with the peculiarities of the climate into which they have come, and not knowing how to adapt themselves to the new conditions, readily become their prey.

## Summary

The climate of the Russian Far East affects all branches of the economic life and activity of the population. If we divide the Russian Far East into separate economic regions, it will be seen that they fully coincide with the climatic provinces and determine not only the present economic conditions, but the future possibilities as well.

*Fishing* is one of the principal occupations in the northeastern part of the Russian Far East. The climate influences this activity, not only affecting the catch, but the drying of the fish. The climate factors are: dampness, large number of cloudy days, fogs, long winter, freezing of the harbors, strong winds.

*Cattle and Animal Breeding.*—In the region of the Chukchi, reindeer breeding is the chief occupation. Among the unfavorable effects of climate are: severe and snowy winters, very hot summers. Cattle breeding in the Amur Province is hampered by the following climatic conditions: heavy summer rains and lack of sunshine, with consequent dearth of nourishing herbs. In the Maritime provinces mild climate and oceanic winds, the latter driving away mosquitoes, are among the favorable climatic conditions.

*Hunting.*—Among the indirect climatic influences the character of vegetation which is determined by climate must be marked. The direct influences are: species of animals and quality of furs, severity of climate, formation of ice crust, sleet, storms, etc., affecting the migration of animals.

*Agriculture.*—In the Okhotsk, Kamchatka, Chukotsk regions sharp oscillations of temperature, humidity, fogs, etc., preclude the possibility of agriculture. In the Ussuri and Amur provinces, where climate is milder, agriculture is considerably developed, permitting even the cultivation of rice.

Customs, houses, and food, especially the latter, are affected by climate. In agricultural regions bread is the chief food; fish and meat, on the other hand, constitute the chief food where fishing and hunting predominate. Among the Chukchi reindeer constitute almost the only food.

The effect of climate upon religious beliefs is seen from the worship of rocks, trees, mountains, elements of wind, rain, thunder, etc.

*Health.*—The long and severely cold winter which is common over the

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largest part of the Russian Far East is most trying upon the population. The healthiest region is Ussuri. Okhotsk is the least healthful because of the excess of cloudiness and winds. In the northern parts of the Russian Far East the prolonged darkness, as well as the low temperature, are very trying, and in summer fogs and exceeding cloudiness along the coast depress and affect the population. The hot days decrease the appetite and affect the digestive system. Hot and humid climate tends to the development of micro-organisms.

*Diseases.*—Lung diseases are especially common throughout the Russian Far East, and occur especially in winter. In the Amur and Maritime provinces diseases of stomach, as a result of unripe food, also of the difference between the temperature of the day and night, are common. An indirect climatic cause of diseases is food, as, for example, badly salted animal fat, which causes internal catarrh. In the eastern parts of the Russian Far East humidity accounts for rheumatism. Diseases of eyes, often resulting in total blindness, are very frequent in the north and northeast, and are due to the dazzling cover of snow and to smoke indoors. In the Okhotsk-Kamchatka region psychic and nervous disorders are prominent and occur as a result of the long monotonous winter and absence of bright sunny days.

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# THE FORMATION OF A NEW ISLAND IN THE MISSISSIPPI RIVER[1]

CHARLES A. SHULL
*University of Kentucky*

While engaged in studying the vegetation of the bluffs in the vicinity of Columbus, Kentucky, in August, 1919, my attention was called to an island which had been forming in Number 5 Chute of the Mississippi River during the preceding six years. This chute separates Island Number 5, better known as Wolf Island, from the Missouri bank of the river just south of Belmont. The peculiar history of the island led me to visit it, and as the information regarding it was confirmed from authentic sources, the facts seem worth recording.

The island lies about a half mile west of the main channel of the river, and somewhat nearer to the Missouri side of the chute than to Wolf Island. It has grown very rapidly since deposition began, and is now nearly three fourths of a mile in length, and about an eighth of a mile in average width. The area, roughly estimated, is about 60 acres, and it stood then high enough to require a 43-foot stage of the river to inundate it.

The soil is a very light-colored sandy silt, such as is known along the river as a cottonwood soil. And the island is a veritable cottonwood thicket, with a most beautiful growth of young trees from 4 to 8 inches in diameter and 30 to 40 feet tall. The trees stand very close together and form very nearly a pure growth. The only other tree occurring is the willow, and there are probably not a hundred of them on the whole island. The trees give one the impression of uniformity in size and height that might arise from a single season's seeding.

It does not seem possible that an island of this size, and with such a fine growth of trees, could have formed in six years; but the history is well known locally, and there is no doubt as to its correctness. During March, 1913, there was a very unusual combination of storms and rainfall over much of the eastern half of the drainage basin of the Mississippi River. North of the Ohio River, from the western boundary of Indiana eastward to the Appalachians, the rainfall between March 22 and 28 was from six to eleven inches. This tremendous precipitation led to very destructive floods, as at Dayton, Ohio, and to a very high river stage throughout the Mississippi Valley south of Cairo.

The crest of the flood passed Cairo from April 4 to 8, during which time the river stood at 54.7 feet. It was during the recession of this great flood

[1] Contributions from the Botanical Laboratories of the Univ. of Kentucky No. 5.



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that a big barge was stranded on a rock bar in Number 5 Chute. This barge formed the original obstruction to the current which caused deposition. It lies completely buried in soil near the head of the island. (See Fig. 1.)

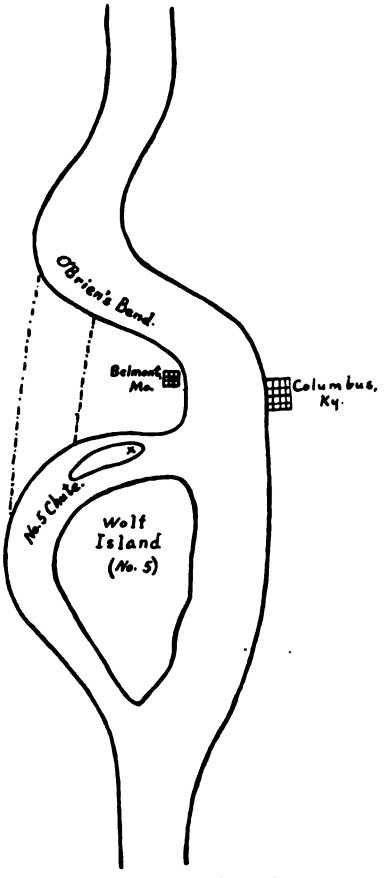


FIG. 1. Sketch map of No. 5 chute and vicinity. The point X represents the position of the stranded barge.

Every year since that time during flood stages of the river the island has increased rapidly in size. I am indebted to Mr. J. L. Kendall, observer of the Weather Bureau at Louisville, for the flood data presented. The crests of the floods at Cairo for each year since 1913 up to 1920 are shown in the table:

The crest of each flood usually reaches New Madrid, Missouri, about a day later than Cairo, and the stage is usually 8 to 10 feet lower at New Madrid. As Columbus lies about one third of the distance to New Madrid below Cairo, the crests would probably average a couple of feet lower than at Cairo. The island has been built by not more than a dozen periods of

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deposition. The floods still frequently cover the island, and each time it is inundated its area and height are materially increased. The last flood recorded was a very long one. The river reached a stage of 43.3 feet on March 18, and from that time until May 9 the island was constantly under water, except for several days, April 21–23, when the stage averaged 42.4 feet. This 1920 flood is the longest continuous period of deposition the island has experienced. From notes taken in June, 1920, by Mr. R. C. Summers, of Columbus, Kentucky, a month after this long flood subsided, the deposit during this period must have been 16 to 18 inches deep, or even more. All traces of under vegetation were destroyed, for, as Mr. Summers comments, "there is not a weed or a sprig of grass on the island." I am also indebted to Mr. Summers for the photographs.

*Flood crests of the Mississippi, 1914–1920*

| | | | |
|---|---|---|---|
| 1914. | April 10–11 | 41.3 | feet |
| 1915. | Feb. 11–13 | 45.6 | " |
| 1916. | Jan. 18–19 | 45.7 | " |
| | Feb. 4 | 53.4 | " |
| 1917. | March 25–27 | 49.2 | " |
| | April 4–5 | 50.1 | " |
| | June 16–17 | 44.6 | " |
| 1918. | Feb. 25–26 | 39.8 | " |
| 1919. | March 24 | 48.5 | " |
| | Dec. 20–21 | 42.1 | " |
| 1920. | March 31 | 51.4 | " |
| | May 1–2 | 49.5 | " |

There is a reason for the very rapid deposition of silt in this channel during floods, and reference to the accompanying map (Fig. 1) will make the explanation clear. Just above Belmont, Missouri, the Mississippi sweeps eastward in a great bend known as O'Brien's Bend, and then turns southward past Columbus. At the time of the greatest floods the river cuts straight across behind Belmont and flows down the lower part of Number 5 Chute, west of Wolf Island. This channel is just about in line with the river above O'Brien's Bend. At a time when the river is high, therefore, the upper part of Number 5 Chute forms a cross-channel between two main channels of the river. It carries "dead water" which is unable to carry its load, and much of the sand and silt is dropped upon this new island. The tendency of the river indicates that it may straighten its channel at some future flood by cutting across behind Belmont, leaving the village on an island, and putting the main channel west of Wolf Island again, as it was formerly, instead of in front of Columbus.

In June, 1919, Mr. Martin Keirce took up his abode on the island and applied for a patent to the land from the government under the homestead laws of Missouri. He had cleared a few acres in the heart of the island a

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couple of months previous to my visit, had piled the cottonwood poles around the edge of his little farm, and wired them down in position to check the currents and aid deposition at each new flood. He kindly took me over the island and pointed out to me approximately the place where the barge is buried near the head of the deposit. After the flood of 1920 Mr. Summers found that the iron bed in Mr. Keirce's shack was buried in solid earth up to the springs, and the cook stove half buried in sediment. Figure 2 shows

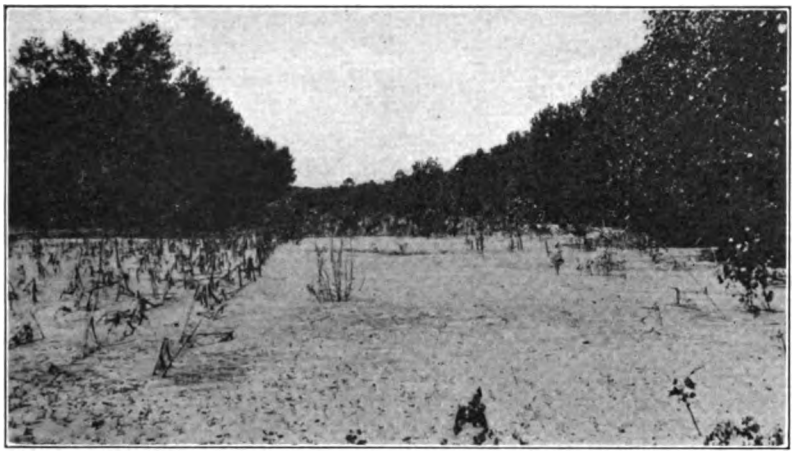

FIG. 2. Clearing, showing the silt deposit of 1920. Cottonwood forest in background and on right. (Photo by Summers.)

the clearing after the flood, with the tops of the corn stalks showing above the deposits.

The channel on the north side of this new island is now beginning to fill, and a younger belt of cottonwoods is forming on that side. On the opposite side of the chute against the Missouri bank there is a mixture of cottonwoods and willows, the willows breast high, and the cottonwoods about three fourths as tall. It seems probable that before many years the island may be joined to the Missouri mainland.

The beautifully even height of the cottonwoods in local areas, not only on this island, but on many young flood-plain deposits and mud flats along the river, is very striking. Terrace-like vegetation, mostly willows and cottonwoods, sometimes several stratifications, are frequently to be observed. People who live along the river think that the trees have come at least in some cases from a single year's crop of seedlings.

The floods kill young trees if they are completely submerged for too long a time. But if the floods are not high for several years in succession, the seedlings of some one year will become tall enough to stand above even the

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highest waters. Being of the same age, equally crowded in thickets, they are usually rather uniform in size and height, producing very beautiful terraces.

It is probable that the history of most islands in the Mississippi is unknown. This new island is of interest because it gives one a concrete idea of the rapidity of deposition under favorable conditions, and its history is certainly unique.

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# A BOG FOREST[1]

George B. Rigg
*University of Washington*

In a previous paper (4, 1917) the writer has described forest succession in Puget Sound sphagnum bogs, and in other papers (4, 1913; 1914; 1919) has listed the trees growing in various sphagnum bogs of the Puget Sound region and Alaska. All of these are comparatively early stages in bog succession. None of them have reached a stage where the forest is dominant.

An area of about three acres near Victoria, British Columbia, shows a very late stage where the forest has become the dominant vegetation, and sphagnum is no longer found living. This area was visited in July, 1920, and a more careful study was made during several visits to it at various times in July, 1921. The area is at present bordered on the south by a meadow, on the east and north by Lost Lake, and on the west by the Patricia Bay line of the Canadian National Railway.

The forest consists of a pure stand of lodge-pole pine, *Pinus contorta.* The trees are of good size for this species, many of them being 20 to 30 feet tall and 6 to 10 inches thick at the base. A few are 12 inches thick. The stand of trees is very dense over nearly all of the area, and many young trees have been killed by the shade of the taller ones. The trunks of these trees are straight and slender. They do not have the scrubby form that this species does on rocky, exposed places, nor the stunted appearance that it has in the early stages of forest succession in Puget Sound bogs. Very few pine seedlings were found, and these only on the border along the west side, where the forest was cleared a few years ago when the railroad was built, and Nature was then allowed to take her course again.

Lodge-pole pine is common on this portion of Vancouver Island. It is found around lakes, both in swampy places and on rocky shores, and on the thin soil of rocky hills. It is found practically to the top of Mount Benson, near Nanaimo. Glendenning (1, 1918) says that it is frequent in bogs and on gravel ridges in the Cowichan district on Vancouver Island. Whitford and Craig (5, 1918) state that this species is general throughout the province of British Columbia, from the international boundary to the Yukon drainage, being found at an altitude of 5,000 to 6,000 feet, and attaining a height of 50 to 75 feet and a diameter of 12 to 24 inches.

The undergrowth in the bog forest under consideration consists of a dense thicket of Labrador tea, *Ledum groenlandicum,* and salal, *Gaultheria shallon.*

[1] Read at the joint meeting of the Ecological Society of America and Western Society of Naturalists, Salt Lake City, June 23, 1922.



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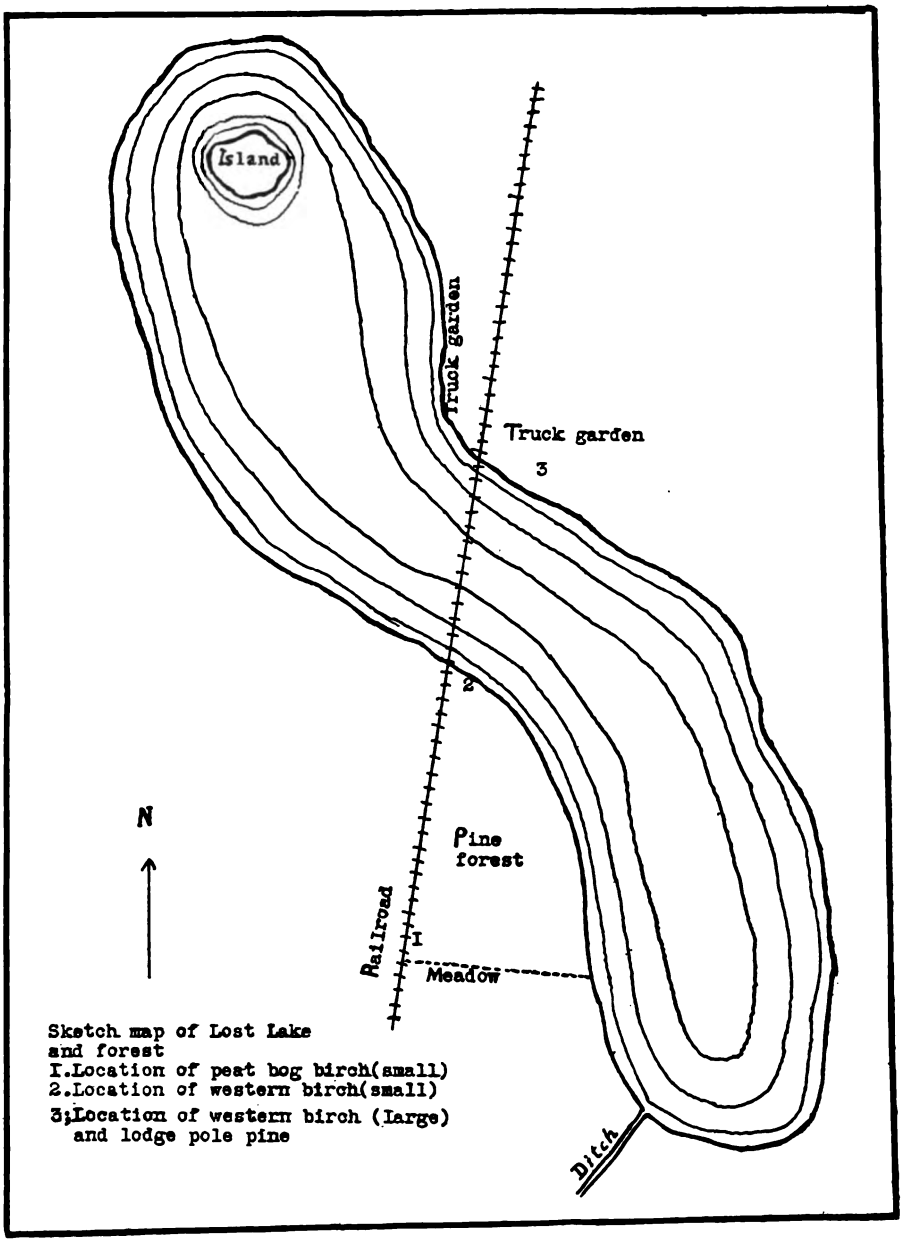


FIG. 1. Sketch map of Lost Lake, showing the location of the pine forest and birch areas.

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Both of these are general throughout the forest, though the salal is taller and more abundant in the occasional places 15 to 25 feet in diameter where the growth of trees is less dense. Vigorous young salal plants are very numerous, most of them growing from the long horizontal roots, characteristic of the species. It is increasing rapidly.

Labrador tea forms a dense growth also and is very tall. Much of it is 6 feet high, and in places it grows almost as a vine, clambering up among the salal and pines to a height of 12 feet in some cases. This species is very characteristic of sphagnum bogs throughout the Puget Sound region and is very common in a bog (Rithet bog) only a few miles from this forest. It is reported by Glendenning (1, 1918) under the synonym of *L. latifolium* in the bogs in the Cowichan district.

This species is not increasing to any great extent in the bog forest under discussion. Young plants are scarce. The ones found are mostly growing from the running stems and roots that characterize the species in bogs. The leaves on the new growth of the taller specimens are larger and less woolly than on the older portions. This is the condition usually seen where this plant grows on the borders of bogs, outside of the area in which sphagnum is dominant. While Labrador tea is thus practically at a standstill, salal is advancing rapidly—a veritable conquering host. The *Pinus-Gaultheria-Ledum* association is dominant, but the first and third members of the association seem to have reached a practically static condition.

Only one other species characteristic of sphagnum bogs was found by the writer in this bog forest. This is the peat bog birch, *Betula glandulosa,* a few specimens of which are found in the extreme southwest corner. They are from 6 to 12 feet tall. This birch is common in and around the Rithet bog only a few miles distant. It is also common in and around certain sphagnum bogs in the Puget Sound region. Newcombe (2, 1921) states that this species is rare in the Victoria region, being reported from Alberni only, except as noted above. He says that it was much more abundant around Lost Lake in 1894 and also in 1908 than it is now. He states also (2, 1921) that the tideland spruce is found in the Lost Lake forest near the specimens of peat bog birch. This spruce is found in many Puget Sound sphagnum bogs.

Except around the margins, plants other than pine, salal, and Labrador tea are not common. Young specimens of hardhack, *Spiraea douglasii,* are occasionally found, only a few being mature enough to blossom. Small specimens of cascara, *Rhamnus purshianna,* are occasional, but none seen within the forest were more than 3 feet tall. Other plants occasionally found are black-cap, *Rubus leucodermis;* evergreen blackberry, *R. laciniatus;* fireweed, *Epilobium angustifolium;* bed straw, *Galium* sp.; nettle, *Urtica* sp., and velvet grass, *Holcus lanatus.* Several species of mosses were found growing on the substratum, but no living sphagnum was found, though careful search

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was made for it. Newcombe (2, 1914) found sphagnum along the lake on the edge of this area a few years ago.

On the south side the forest ends abruptly in a straight line, where it is bordered by the meadow. The clearing here has been done so completely that no trace of the forest remains. The railroad along the west side of the bog is on a trestle. Since the clearing of this right-of-way at the time of the construction of the railroad, less than ten years ago, it has been but little disturbed and salal and Labrador tea are making a vigorous growth, with pine seedlings numerous and thrifty. Seedlings of alder, *Alnus oregona,* are also occasionally found.

FIG. 2. Margin of the forest along the railroad, showing dense growth of Labrador tea on the cleared portion. Young alders in the foreground.

In the northwest corner are a few small specimens of the western birch, *Betula occidentalis.* None of these are more than 5 feet tall, though on the north side of the lake in an area which is now cleared, but was evidently similar to the one under discussion, specimens 8 inches in diameter and 20 feet tall are still standing, and stumps 24 inches in diameter are still seen.

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Newcombe (2, 1921) says that this species is rare on Vancouver Island, being reported from only two locations, these both near Victoria.

Along the shore of the lake, which forms the north and east border of the bog, is a dense thicket of deciduous trees and shrubs. The crab-apple, *Pyrus rivularis,* so commonly found on the borders of bogs in the Puget Sound region, is dominant among these. The individuals are numerous and some of them are 15 feet tall. A few cascara trees of about the same size are also found, and dogwood, *Cornus occidentalis,* of similar size is fairly abundant. There are also a few specimens of elder, *Sambucus* sp.

In the tension line between this thicket and the bog forest are a few conifers other than pine. Nearly all of the specimens are less than 6 feet tall. The Douglas fir, *Pseudotsuga taxifolia,* and western hemlock, *Tsuga heterophylla,* occur occasionally. The white fir, *Abies grandis,* is more common, specimens from 1 to 6 feet tall being fairly abundant in places. The edge of the forest seems to be static, so far as the pines are concerned, no pine seedlings being found in the thicket.

The lake margin bordering on this thicket shows three fairly distinct zones. The outer one is composed of a dense growth of two pond-weeds, *Potamogeton* sp. One of these species has floating leaves, and among these the common duckweed, *Lemna minor,* is common. The second zone consists of the yellow pond lily, *Nymphaea polysepala,* a bulrush, *Scirpus* sp., growing from 6 to 10 feet tall, and the cat-tail, *Typha latifolia.* The third zone occupies the margin of the water. It is made up mainly of water celery, *Oenanthe sarmentosa,* and water parsnip, *Sium suave,* with some purple marsh locks, *Comarum palustre,* and buck bean, *Menyanthes trifoliata,* and a buttercup, *Ranunculus loffi.* A liverwort, *Ricciocarpus* sp., forms numerous rosettes on the mud. The duckweed is found in the last two zones as well as the first.

The substratum on the margin of the lake is firm at the surface, and the zones of vegetation.

The surface of the substratum within the pine forest is thickly covered shallow margin of the lake is being slowly filled by the growth of these three with pine needles mixed with a small amount of other material of vegetable origin. Under the surface decay has begun. The depth of the layer of pine needles in various stages of decay is from 6 to 12 inches. Beneath this is a layer of old sphagnum usually 12 inches or more thick. Six holes were dug in widely separated portions of this forest and the same conditions were found in all. Leafy stems of sphagnum an inch or more long were still intact. Microscopic examination of several specimens from each hole was made, and in all cases the hyaline cells of sphagnum, with their characteristic markings, were easily recognized.

Samples taken with a Davis peat sampler showed conditions similar to those found in sphagnum bogs of Washington, Oregon, and British Columbia in which living sphagnum still forms much of the surface of the substratum.

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Hard soil was not reached anywhere in the forest at a depth of 20 feet. In the adjoining meadow blue clay was found at a depth of 18 to 20 feet. The substratum below the sphagnum layer was everywhere very watery. Samples taken at a depth of 16 to 20 feet in the forest were brown and plastic, and, when rolled into balls and dried in the sun, they shrank to about half their original size and became very hard. Above this depth the samples were more or less fibrous and occasionally contained small particles of rotten wood. Small roots, together with material resembling the leaves of *Carex,* made up much of the solid material in these samples. Newcombe (2, 1914) states that the railway engineers did not find a sufficiently solid foundation for their roadbed, even at the depth of 100 feet.

A drainage ditch extends southwestward from the southwestern side of the lake, south of the forest. It was dug in 1894 (Newcombe, 2, 1914). It was learned that the level of the lake has been lowered by means of this ditch. On the north side of the lake, both east and west of the railroad, there are truck gardens on which cabbage, celery, head lettuce, carrots, parsnips, and mangels were seen growing. These areas are only 2 to 3 feet above the present level of the lake, and are stated to have been formerly covered with water and to be still very wet during the rainy season. It is probable that forest succession has been hastened somewhat by this drainage, though it seems impossible that the dense pine forest can be entirely due to this.

The Rithet bog, situated on the Rithet farm only a few miles from the area just described, furnishes some interesting comparisons. References to this bog have already been made. The area around this bog has been cleared and some of it is used for pasture. It has also been drained, but apparently with less success than has attended the efforts at Lost Lake. Water stood in the ditch that had been dug along the north side of it, but no movement of the water could be detected during any of the visits made to it. The sphagnum in the bog is mostly dead, though there are a good many small areas on which it grows during the rainy season and dries up during the summer.

The bog has a flora similar to that of Puget Sound bogs in Washington. Labrador tea; swamp laurel, *Kalmia polifolia;* sundew, *Drosera rotundifolia;* cranberry, *Oxycoccus oxycoccus;* cotton grass, *Eriophorum* sp.; the peat bog birch, and the lodge-pole pine are abundant. All of this list except the peat bog birch are mentioned by Glendenning (1, 1918) as being found in the bogs in the Cowichan region. A few small specimens of Douglas fir are also found. Other plants found in the bog, but not characteristic of a true sphagnum bog stage of succession, are the common brake, *Pteridium aquilinum,* fireweed, hardhack, and salal. The birches along the drainage ditch form a dense growth 10 to 15 feet high, but farther into the bog they are smaller and more scattering.

At the south side of the bog there is a strip two to four rods wide on which there is a practically pure stand of lodge-pole pine. The conditions in

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this strip both as to flora and substratum are strikingly similar to those in the forest at Lost Lake.

Five lines of evidence point to the conclusion that the Lost Lake area is a case where the forest has been a successful invader of a sphagnum bog, finally becoming the dominant vegetation. (1) The dominance of the pines. (2) The abundant survival of Labrador tea and the occasional survival of the peat bog birch. (3) The presence of the layer of dead sphagnum. (4) The similarity between the deeper layers of the substratum in this area and the corresponding layers of bogs in Washington and Oregon where living sphagnum still forms much of the surface. (5) The similarity between this bog and the strip of forest along the edge of the Rithet bog which still has a characteristic bog flora.

It must be remembered, however, that drainage and clearing of the surrounding area, both tending to drier conditions, have undoubtedly hastened succession.

The writer was aided in this work by a grant from the research funds of the American Association for the Advancement of Science. He acknowledges, with pleasure, his indebtedness to Dr. C. F. Newcombe for information about this bog based on observations made by him in former years.

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# A DISTRIBUTIONAL AND ECOLOGICAL STUDY OF MOUNT RAINIER, WASHINGTON[1]

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*United States Biological Survey*

## Physiography

Mount Rainier is composed almost wholly of basaltic rock built up from the cinders, bombs, and liquid lava of its own eruptions, granite appearing in but few scattered places. An explosion which blew off the top of the mountain is supposed to have reduced its height some 2,000 feet, and to have left a capacious crater nearly three miles in diameter from north to south. Subsequently two small cinder cones filled this crater and, adding to their height, formed a low rounded dome which is the mountain's summit at present (Matthes, 1914, p. 7).

According to Matthes the total area of the glaciers of Mount Rainier is forty-five square miles, ". . . an expanse of ice far exceeding that of any other single peak in the United States." These glaciers, more than twenty-five in number, have had a profound effect on the topography of the mountain, grinding out deep channels on its sides, and leaving huge wedges of rock in relief between. The wedges, heading in sharp points near the summit, give place, as one descends, to grassy and flower-covered meadows. Lower

[1] During the summer field season of 1919 biological field work was carried forward in Mount Rainier National Park by the Bureau of Biological Survey of the U. S. Department of Agriculture, the State College of Washington, and the National Park Service of the U. S. Department of the Interior. Attention had been directed to Mount Rainier for several reasons. The biological survey of the State of Washington had progressed to a point where a study of one of the important mountains in the Cascade chain lying wholly west of the main summit was desirable; and Mount Rainier is the most massive as well as the highest of the four principal mountains (Baker, Glacier, Rainier, St. Helens) fulfilling this description. It was anticipated also that fewer modifications in natural conditions as a result of interference by man would be observable in the National Park than elsewhere; and it was thought that the results of the study would be of interest to a wider circle than would otherwise be the case.

The field party at different times included the following: J. B. Flett, Senior Park Ranger, National Park Service; Stanton Warburton, Jr., Tacoma, Washington; William L. Finley and family, Portland, Oregon; J. W. Hungate, State Normal School, Cheney, Washington; Professor William T. Shaw, State College of Washington; George G. Cantwell, Biological Survey, Puyllup, Washington; Stanley G. Jewett, Biological Survey, Portland, Oregon; and the writer, who was in general charge of the work.

A comprehensive account of the birds and mammals of Mount Rainier, to be published by the National Park Service, has been completed recently by Professor William T. Shaw and the writer. Free quotation has here been made from the introductory paragraphs of the larger work.



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down appear deep, glacier-carved canyons and high, steep-sided ridges, all heavily forested. Flowing from the ends of the various glaciers are a number of rivers, mostly muddy white in color, which become swollen and turbulent in midday during the summer season from the melting of ice and snow.

The climate of Mount Rainier is of the warm humid type, partaking more of that of the coast strip of Washington than of the arid eastern portion of the State. A conspicuous feature is the heavy precipitation, the total measured snowfall at Paradise Inn during 1916–17 (789.5 inches) being apparently greater than for any Weather Bureau station in the United States for any entire season, with the single exception of Tamarack, California, in 1906–7 (Fisher, 1919, p. 328). The snowfall appears to be heavier in Indian Henrys Hunting Ground (on the southwest slope of the mountain) and lighter in Summerland (on the east slope) than in Paradise Valley, which is on the south slope. As might be expected, the extremely humid climate of the mountain, and the differences in precipitation on its slopes, exercise an important influence on the occurrence and distribution of its animals and plants.

## Communities of Birds, Mammals, and Plants

### Life Zone, Habitat, and Association

#### *Life Zones*

"As a fundamental expression of progressive change in the amount of heat and water, zonation is the most important feature of vegetation," as one observer has said (Clements, 1905, p. 281). As used by the present writer, a *life zone* is an area inhabited by a more or less definite group of animals and plants limited in its distribution chiefly by temperature. It should be emphasized that classification of living forms by zones or habitats in the present state of knowledge is largely for convenience, and is often quite arbitrary.

#### *Habitats and Associations*

As already stated, moisture relations play an important rôle in relation to the occurrence and distribution of the animals and plants of Mount Rainier. A conception of the situation can be gained by using the *habitat* and *association.* The *habitat,* to adapt and modify somewhat a definition by Clements (1905, p. 292), is an area characterized by some efficient difference in one or more of the direct factors, humidity, water content, light, by virtue of which the fauna and flora are different from those surrounding them. As used by the present writer the term *association* is used for the group of plants and animals of a particular habitat.

A habitat may occupy the same area as that of a life zone; more often it occupies only a part of a zone, or transcends zonal boundaries. The principal plant and animal habitats of Mount Rainier can in the main be classified on a

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moisture basis. A combination of the life zone, mapped on broad lines with temperature as the basic factor, and the habitat with its association, determined chiefly on water relations, should afford a more adequate picture of the distribution of plant and animal life on Mount Rainier than would either alone.

## Life Zones of Mount Rainier

Four life zones are represented on the mountain, the Transition, Canadian, Hudsonian, and Arctic-Alpine. The zones are somewhat obscured as a result of the powerful influence of humidity in western Washington, an influence to which Mount Rainier, lying 12 miles west of the main divide of the Cascade Mountains, is fully subject.

### *Transition Zone*

The Transition Zone occupies the smallest area and is the least important of the zones of the Park. Although Transition elements occur occasionally up to 3,500 or even 4,000 feet at certain points on the west side of the mountain and were noted on the Carbon, Puyallup, Mowich, Nisqually, and other river systems, the Zone can be clearly recognized in the southeastern part of the Park only, where it is found in a limited area (four to six square miles) on Stevens Creek and the Muddy Fork of Cowlitz River below an altitude of 3,000 feet. In this region there occurred in the old Indian days repeated fires which laid waste a great area and profoundly modified the plant and animal population. This burning has evidently favored the upward advance of low zone elements.

Among the plants here indicating Transition Zone, but not necessarily confined to it, are the grand or white fir *Abies grandis,* salal *Gaultheria shallon,* Oregon grape *Berberis nervosa,* western bracken *Pteridium aquilinum pubescens,* red alder *Alnus oregona,* large-leaf maple *Acer macrophyllum,* vine maple *Acer circinatum,* western cottonwood *Populus trichocarpa,* early willow *Salix scouleriana,* western dogwood *Cornus occidentalis,* ocean spray *Sercotheca discolor,* devil's club *Echinopanax horridum,* salmon berry *Rubus spectabilis,* and fetid currant *Ribes bracteosum.* Birds of the Transition include the[2] California quail *Lophortyx californica californica,* Oregon ruffed grouse *Bonasa umbellus sabini,* northern spotted owl *Strix occidentalis caurina,* Lewis woodpecker *Asyndesmus lewisi,* nighthawk *Chordeiles virginianus* ssp., black-headed grosbeak *Zamelodia melanocephala,* yellow warbler *Dendroica aestiva* ssp., western warbling vireo *Vireosylva gilva swainsoni,* Parkman wren *Troglodytes aedon parkmani,* Seattle wren *Thryomanes bewicki calophonus,* and Oregon chickadee *Penthestes atricapillus occidentalis.* Mam-

[2] Permanent residents or summer visitants among the birds, when referred to particular zones or habitats, are assumed to breed therein. The few migrant birds listed are most commonly observed in the particular zone or habitat to which they are referred.

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mals include the wandering shrew *Sorex vagrans vagrans,* Bendire water shrew *Neosorex bendirii bendirii,* raccoon *Procyon lotor pacifica,* mink *Mustela vison energumenos,* little spotted skunk *Spilogale phenax olympica,* Oregon meadow mouse *Microtus oregoni oregoni,* Olympic meadow mouse *Microtus mordax macrurus,* and the muskrat *Fiber zibethicus osoyoosensis.*

### *Canadian Zone*

In this Zone is the heavily timbered area from the Park boundaries (except in the southeastern part of the Park) to 4,500–5,000 feet. This, then, is the area of huge trees of impressive diameter and height, and of mossy forest floor, usually clear of thick underbrush. Progress away from trails is laborious, for creeks and springs, uneven topography, and many huge logs make it difficult to maintain a footing. As a result of the dominating influence of the climax forest of western hemlock *Tsuga heterophylla,* Douglas fir *Pseudotsuga mucronata,* and giant cedar *Thuja plicata,* the growth of all but the most shade tolerant plants is prevented, and consequently the amount of food for birds and mammals is much reduced.

The Zone occupies an area of varying width all around the mountain. The deep-wooded canyons, and ridges between as well, are commonly referable to it, while the amphitheater-like parks on the headwaters of the principal streams belong to the Hudsonian Zone next above.

Plants commonly occurring in the Canadian Zone, in addition to the three trees just mentioned, are as follows: lovely fir *Abies amabilis,* noble fir *Abies nobilis,* lodgepole pine *Pinus contorta,* western white pine *Pinus monticola,* western yew *Taxus brevifolia,* bunchberry or Canada dogwood *Cornus canadensis, Menziesia ferruginea,* mountain ash *Pyrus sitchensis, Pachistima myrsinites,* forest anemone *Anemone deltoidea,* wild bleeding heart *Capnoides scouleri,* alpine beauty *Clintonia uniflora,* Mertens coral root *Corallorhiza mertensiana,* oak fern *Phegopteris dryopteris,* Mertens saxifrage *Saxifraga mertensiana,* and false Solomon's seal *Vagnera sessilifolia.*

The birds include the Harris woodpecker *Dryobates villosus harrisi,* Gairdner woodpecker *Dryobates pubescens gairdneri,* northern red-breasted sapsucker *Sphyrapicus ruber notkensis,* pileated woodpecker *Phloeotomus pileatus abieticola,* western flycatcher *Empidonax difficilis difficilis,* Steller jay *Cyanocitta stelleri stelleri,* western tanager *Piranga ludoviciana,* chestnut-backed chickadee *Penthestes rufescens rufescens,* western golden-crowned kinglet *Regulus satrapa olivaceus,* russet-backed thrush *Hylocichla ustulata ustulata,* and western bluebird *Sialia mexicana occidentalis.* Mammals occurring in this Zone are the Trowbridge shrew *Sorex trowbridgii,* brown bat *Eptesicus fuscus fuscus,* bobcat *Lynx fasciatus* ssp., Cooper chipmunk *Eutamias townsendi cooperi,* beaver *Castor canadensis pacificus,* and snowshoe rabbit *Lepus washingtonii washingtonii.*

It is difficult to make a distinction between Canadian and Transition Zones

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on Mount Rainier because of the uniformity of the Douglas fir-western hemlock-giant cedar forest, which dominates the flora (excepting upper Canadian) in both. The species of birds and mammals listed above do not ordinarily occur above Canadian, though they are all found also in Transition. There are no birds or mammals characteristic exclusively of the Canadian Zone on the mountain.

### *Hudsonian Zone*

At an altitude of approximately 4,500 feet the aspect of the forest changes. The Douglas fir has dropped out somewhat lower down, the lovely fir has become abundant, and now the western hemlock disappears. The trees are reduced in size, and the alpine fir and mountain hemlock, with the lovely fir, dominate the forest. One is now at the lower border of the Hudsonian Zone, which, on the average, embraces the area between 4,500 and 6,500 feet, including the narrow upper portion of the dense woods, as well as the meadow country between the forest and the limit of trees. This area constitutes a belt of varying width, being most extensive in the high country northeast of Mount Rainier, where it includes Grand Park and the Sourdough Mountain district.

This and the next are zones of wonderful scenery; and the Hudsonian Zone, above the narrow forested area, with its happy combination of open grassy park and subalpine flower garden on the one hand, and pinnacle and glacier on the other, is without doubt the most attractive zone on the mountain (see Flett, 1916). The shade of the deep Canadian forest is gone. Groups of handsome spire-like alpine firs and mountain hemlocks are set about the meadow borders or interspersed over the green expanses, always affording plenty of light and moisture to the grass and flowers. There is an abundance of food for birds and mammals, which are more conspicuous and probably more numerous in this Zone than in any other in the Park.

Plants occurring principally in this Zone are mountain hemlock *Tsuga mertensiana,* alpine fir *Abies lasiocarpa,* white-bark pine *Pinus albicaulis,* Alaska cedar *Chamaecyparis nootkatensis,* white heather *Cassiope mertensiana,* red heather *Phyllodoce empetriformis,* Jeffrey shooting star *Dodecatheon jeffreyi,* smooth larkspur *Delphinium glaucum,* avalanche lily *Erythronium montanum,* yellow deer tongue *Erythronium parviflorum,* delicious huckleberry *Vaccinium deliciosum,* small red huckleberry *Vaccinium scoparium,* mountain gentian *Gentiana calycosa,* lungwort *Mertensia laevigata,* ovate salal *Gaultheria ovatifolia,* Nuttall gilia *Gilia nuttallii,* Sitka valerian *Valeriana sitchensis,* green hellebore *Veratrum viride,* squaw grass *Xerophyllum tenax,* Siberian juniper *Juniperus sibirica,* jacobs ladder *Polemonium humile,* mountain dock *Polygonum bistortoides,* subalpine lupine *Lupinus subalpinus,* western anemone or monkey whiskers *Pulsatilla occidentalis,* Suksdorf buttercup *Ranunculus suksdorfii,* and Cusick speedwell *Veronica cusickii.* Among the

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birds of the Zone are the golden eagle *Aquila chrysaetos,* saw-whet owl *Cryptoglaux acadica acadica,* Clark nutcracker *Nucifraga columbiana,* Cassin purple finch *Carpodacus cassini,* western chipping sparrow *Spizella passerina arizonae,* lutescent warbler *Vermivora celata lutescens,* mountain chickadee *Penthestes gambeli gambeli,* Townsend solitaire *Myadestes townsendi,* hermit thrush *Hylocichla guttata sequoiensis,* and mountain bluebird *Sialia currucoides.* The mammals include the red fox *Vulpes cascadensis,* Washington weasel *Mustela washingtoni,* Canada lynx *Lynx canadensis,* mountain lemming mouse *Phenacomys orophilus olympicus,* Rainier meadow mouse *Microtus oregoni cantwelli,* large-footed meadow mouse *Microtus richardsoni arvicoloides,* Rainier pocket gopher *Thomomys douglasii shawi,* Cascade hoary marmot *Marmota caligata cascadensis,* little chipmunk *Eutamias amoenus caurinus,* mantled ground squirrel *Callospermophilus lateralis saturatus,* and cony *Ochotona fenisex brunnescens.*

### *Arctic-Alpine Zone*

At or close to the 6,500-feet contour the Arctic-Alpine Zone is entered. Here belong the conspicuous snow- and ice-covered upper slopes of the mountain, comprising an area of approximately eighty square miles. With its wilderness of glacier, snow-slope, rocky cleaver, beetling cliff, and massive wedge, the scenery of the Arctic-Alpine is of a highly attractive character.

The heaviest snowfall takes place at moderate elevations, most of the glaciers originating in amphitheaters at about 10,000 feet elevation (Matthes, 1914, p. 21).

The Arctic-Alpine is the particular dwelling place of the Sandwort *Arenaria capillaris nardifolia,* two kinds of Indian paint brushes *Castilleja oreopola* and *C. rupicola, Draba aureola,* crow berry *Empetrum nigrum,* alpine buckwheat *Eriogonum pyrolaefolium coryphaeum, Phacelia sericea,* golden aster *Erigeron aureus, Gilia debilis, Hulsea nana,* mountain aster *Oreostemma alpigena,* pigeon-billed lousewort *Pedicularis ornithorhyncha, Pentstemon menziesii,* yellow heather *Phyllodoce glanduliflora,* Lyall lupine *Lupinus lyallii,* snowy willow *Salix nivalis,* Tolmie saxifrage *Saxifraga tolmiei, Smeiowskia ovalis, Spraguea multiceps,* and *Polemonium viscossum.* Four birds, the pallid horned lark *Otocoris alpestris arcticola,* rosy finch *Leucosticte tephrocotis littoralis,* pipit *Anthus rubescens,* and ptarmigan *Lagopus leucurus rainierensis,* and one mammal, the mountain goat *Oreamnos montanus,* also occur in this Zone.

In winter the rocky slopes above timberline, where in summer such animals as the ptarmigan and mountain goat find food, are deeply covered with snow except where the wind exposes the rocky ridges. An alternate freezing and thawing often coats all exposed surfaces with glare ice, which renders food unobtainable and life for birds or mammals of this sort impossible.

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## The Habitats of Mount Rainier

The following habitats are characterized by extreme moisture: stream, stream-border, lake, lake-shore, and swamp. Those having moderate moisture are meadow, forest (including the several strata of vegetation due perhaps principally to light, with associated animal life), and burn. Habitats of deficient moisture or of a rocky type include alpine ridge, pumice slope, and rock-slide. The glacier habitat probably furnishes little available water so is tentatively placed here also.

As noted in the paragraph on Life Zones, page 215, the classification of living forms by zones or habitats, in the present state of knowledge, is largely for convenience, and often quite arbitrary. It will be impossible to give a fully satisfactory account of the distribution and relationships of the plants and animals of Mount Rainier until a thorough ecological survey is accomplished.

### *Habitats Characterized by Extreme Moisture*

*Lake, lake-shore, stream, stream-border, swamp.*—There are few lakes of any size in the Park, the largest being Crater or Mowich Lake northwest of the mountain. Practically all the lakes are glacial tarns, most of them located at altitudes exceeding 4,000 feet. Ordinarily they lie at so great an altitude in the glacier-hewn amphitheaters that their shores are rocky and devoid of conspicuous vegetation, although scenically they are wonderfully attractive.

The turbulent streams of the mountain, fed by glaciers, and becoming much swollen in midday and afternoon when the sun shines, are a conspicuous feature of the Park. Taking origin from the snouts of the glaciers or from springs or swamps on the meadows, the streams radiate from the mountain in all directions, and give rise to not a few waterfalls and cascades of extraordinary beauty.

True swamps are of limited extent and fade imperceptibly into stream-borders on the one hand and meadows on the other. Restricted areas about Longmire Springs, Reflection Lakes, and Mountain Meadows may be classified here. There are also swampy tracts at intervals along some of the streams of the Park, as Tahoma Creek, Ohanapecosh River, and White River.

Willows of several species, *Salix commutata, S. barclayi, and S. lasiandra,* grow on the shores of some of the lakes at more moderate altitudes, as do also *Kalmia glauca microphylla* and the common horsetail *Equisetum arvense.* Occurring characteristically in the immediate vicinity of streams are the alpine monkey flower *Mimulus alpinus,* Lewis monkey flower *Mimulus lewisii,* yellow fireweed *Epilobium luteum, Cardamine kamtschatica,* and silky willow *Salix sitchensis.* Swamp plants include the cat-tail *Typha latifolia,* skunk cabbage *Lysichiton camtschatcense,* swamp star flower *Trientalis arctica, Hypericum anagalloides,* and the Jeffrey shooting star *Dodecatheon jeffreyi.* Among the birds of these moist habitats are the red-breasted merganser

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*Mergus serrator,* harlequin duck *Histrionicus histrionicus,* pintail *Dafila acuta,* great blue heron *Ardea herodias fannini,* semipalmated sandpiper *Ereunetes pusillus,* spotted sandpiper *Actitis macularius,* belted kingfisher *Ceryle alcyon,* water ouzel *Cinclus mexicanus unicolor,* and Lincoln sparrow *Melospiza lincolni.* Mammals include the navigator water shrew *Neosorex navigator navigator,* Bendire water shrew *Neosorex bendirii bendirii,* Gibbs shrew mole *Neurotrichus gibbsii gibbsii,* raccoon *Procyon lotor pacifica,* mink *Mustela vison energumenos,* otter *Lutra canadensis pacifica,* large-footed meadow mouse *Microtus richardsoni arvicoloides,* muskrat *Fiber zibethicus osoyoosensis,* and beaver *Castor canadensis pacificus.*

### *Habitats Characterized by Moderate Moisture*

*Meadow.*—The Hudsonian Zone meadows of Mount Rainier are second only to its glaciers in interest, for they are among the most famous natural flower gardens in the world. Meadows of limited extent occur in the Canadian and Arctic-Alpine Zones also. The Hudsonian Zone meadows are extensive and include a number of well-known parks just below timberline, as Paradise Park, Grand Park, Spray Park, Sunset Park, and St. Andrew's Park.

The principal Hudsonian meadow plants have been already mentioned (see pages 218–219). Canadian meadow forms include the rosy spiraea *Spiraea densiflora, Trautvetteria grandis,* lousewort *Pedicularis bracteosa,* and *Limnorchis leucostachys.* The meadows of the Arctic-Alpine, which grade by imperceptible degrees into the Arctic-Alpine ridges of deficient moisture (see page 224), exhibit *Smelowskia ovalis,* Lyall lupine *Lupinus lyalli, Saxifraga caespitosa,* snowy willow *Salix nivalis, Arenaria verna,* crowberry *Empetrum nigrum,* golden aster *Erigeron aureus, Solidago algida,* lousewort *Pedicularis contorta,* alpine buckwheat *Eriogonum pyrolaefolium coryphaeum,* and *Agoseris alpestris.* Among meadow birds are the rufous hummingbird *Selasphorus rufus,* pallid horned lark *Otocoris alpestris arcticola,* western meadow lark *Sterna neglecta* ssp., Brewer blackbird *Euphagus cyanocephalus,* Savanna sparrow *Passerculus sandwichensis alaudinus,* and western robin *Planesticus migratorius propinquus.* Meadow mammals include the coyote *Canis latrans lestes,* mountain lemming mouse *Phenacomys orophilus olympicus,* Oregon meadow mouse *Microtus oregoni oregoni,* Rainier meadow mouse *M. oregoni cantwelli,* Rocky Mountain meadow mouse *M. mordax mordax,* Olympic meadow mouse *M. m. macrurus,* large-footed meadow mouse *M. richardsoni arvicoloides,* Rainier pocket gopher *Thomomys douglasii shawi,* and jumping mouse *Zapus trinotatus trinotatus.*

*Forest.*—This habitat is one of the most conspicuous on the mountain. The forest is of a dense and somber character. "The trees, pushing upward for light, are very tall and free from limbs for more than half their height. Their tops form a continuous cover which the sunshine rarely penetrates, and

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on which the light snows of early winter fall and melt, without reaching the ground. Even in midsummer the light is soft and shaded, and the air cool and humid" (Allen, 1916, p. 1). Exclusive of burns, the heavily forested tract embraces the area between the Park boundaries and 5,000 feet. The principal plants are, of course, trees, including the Douglas fir *Pseudotsuga mucronata,* western hemlock *Tsuga heterophylla,* lovely fir *Abies amabilis,* noble fir *Abies nobilis,* and giant cedar *Thuja plicata.* The western white pine *Pinus monticola* occurs at intervals through the forest, and at higher levels there is a considerable quantity of Alaska cedar *Chamaecyparis nootkatensis,* as well as some mountain hemlock *Tsuga mertensiana.* On the northeast side of the mountain the Engelmann spruce *Picea engelmanni* occurs commonly in this habitat. The lodgepole pine *Pinus contorta* is occasionally encountered, occurring principally in the White River region.

In a few places the upper boundary of the forest habitat coincides with that of the Canadian Zone, but normally the deep, shady wood extends into the lower Hudsonian Zone for about 500 feet of vertical altitude.

The forest habitat possesses height as well as breadth, and can be subdivided vertically into three main strata or layers, a ground stratum (including the forest floor), an intermediate stratum, and an uppermost stratum.

The forest floor is carpeted with mosses of two principal species, *Hypnum robustum* and *H. splendens.* Growing on this forest floor appear shade-tolerant species of plants, ranging from a few inches to several feet in height, able to live in the depths of the forest. Here are the bunch berry *Cornus canadensis,* alpine beauty *Clintonia uniflora,* bird's-foot bramble *Rubus pedatus,* vanilla leaf *Achlys triphylla,* forest anemone *Anemone deltoidea,* huckleberries *Vaccinium parviflorum,* etc., vine maple *Acer circinatum,* devil's club *Echinopanax horridum,* false Solomon's seal *Vagnera sessilifolia,* and thimbleberry *Rubus parviflorus.* In this ground stratum live the Oregon ruffed grouse *Bonasa umbellus sabini* and the western winter wren *Nannus hiemalis pacificus;* and the hermit thrush *Hylocichla guttata sequoiensis* and russet-backed thrush *Hylocichla ustulata ustulata* spend most of their time here. Almost all the forest mammals except those which live principally in trees, like the flying squirrel, or in the air, like the bats, are found in this ground stratum. The woodrat *Neotoma cinerea occidentalis,* red-backed mouse *Evotomys gapperi saturatus,* Cooper chipmunk *Eutamias townsendi cooperi,* and Washington varying hare *Lepus washingtonii washingtonii* are numbered among these ground dwellers. Many other mammals are regularly found on the forest floor, including the dusky shrew *Sorex obscurus setosus,* black bear *Ursus americanus,* marten *Martes caurina caurina,* two kinds of weasels *Mustela washingtoni* and *M. streatori,* bobcat *Lynx fasciatus* ssp., white-footed mouse *Peromyscus maniculatus oreas,* and Columbian black-tailed deer *Odocoileus columbianus.*

As the intermediate stratum is entered, the number of plants and mammals

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undergoes a marked decrease, while the number of birds increases. Practically the only conspicuous plants able to live in the upper strata are the lichens, chiefly *Sticta pulmonaria* and several species of *Usnea*. The Douglas squirrel *Citellus douglasii douglasii* and flying squirrel *Glaucomys sabrinus fuliginosus* are the principal mammalian inhabitants. These are bona fide residents of the intermediate stratum, though they are active on the ground, too. Many other mammals occasionally or often climb trees, for example the black bear, fisher *Martes pennanti pacifica*, marten, bobcat, cougar *Felis oregonensis oregonensis*, and Cooper chipmunk. Birds of the intermediate stratum include the band-tailed pigeon *Columba fasciata*, sharp-shinned hawk *Accipiter velox*, western goshawk *Astur atricapillus striatulus*, northern spotted owl *Strix occidentalis caurina*, saw-whet owl *Cryptoglaux acadica acadica*, screech owl *Otus asio* ssp., horned owl *Bubo virginianus* ssp., Harris woodpecker *Dryobates villosus harrisi*, Sierra hairy woodpecker *D. v. orius*, Gairdner woodpecker *Dryobates pubescens gairdneri*, Alaska three-toed woodpecker *Picoides americanus fasciatus*, northern red-breasted sapsucker *Sphyrapicus ruber notkensis*, pileated woodpecker *Phlootomus pileatus abieticola*, tawny creeper *Certhia familiaris occidentalis*, western flycatcher *Empidonax difficilis*, Steller jay *Cyanocitta stelleri stelleri*, gray jay *Perisoreus obscurus griseus*, western evening grosbeak *Hesperiphona vespertina montana*, western tanager *Piranga ludoviciana*, slender-billed nuthatch *Sitta carolinensis aculeata*, red-breasted nuthatch *Sitta canadensis*, and mountain chickadee *Penthestes gambeli gambeli*. There are, of course, no hard and fast lines bounding any of these strata, and birds may and often do range freely into contiguous divisions. The American crossbill *Loxia curvirostra minor* and white-winged crossbill *L. leucoptera*, and the Townsend warbler *Dendroica townsendi* are perhaps more often found in the uppermost than in the intermediate stratum. The western golden-crowned kinglet *Regulus satrapa olivaceus* and chestnut-backed chickadee *Penthestes rufescens rufescens* are found in both intermediate and uppermost strata. With the possible exception of certain bats, no mammals occur exclusively in the uppermost stratum, though the Douglas squirrel and flying squirrel doubtless range into it quite freely.

Although deciduous trees, such as alders, cottonwoods, etc., are scarce within the Park, one group of birds, including the downy woodpecker, western warbling vireo, yellow warbler, and Oregon chickadee, prefers the deciduous forest habitat.

*Burn.*—Before the regulations governing the Park went into effect severe fires swept parts of the subalpine forest. There have resulted tracts of standing dead stubs or "ghost trees" with much fallen timber and brush between. A large area on the Muddy Fork of the Cowlitz River and on Stevens Creek has also been repeatedly burned (see, page 216). The alpine burns recover very slowly, there being little apparent change within the last

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thirty years (Allen, 1916, p. 5). At low elevations the forest recovers more rapidly. The importance of maintaining adequate fire protection is obvious.

Destruction of the climax forest throws back the vegetation into an earlier stage of development in which, disregarding the minor stages, appear various species of brush and herbs as fireweed *Epilobium angustifolium,* western bracken *Pteridium aquilinum pubescens,* blackberry *Rubus macropetalus,* thimbleberry *Rubus parviflorus,* running pine *Lycopodium clavatum,* huckleberries *Vaccinium* sp., subalpine lupine *Lupinus subalpinus,* and squaw grass *Xerophyllum tenax.* Food of certain kinds is more abundant here than in the forest, and we find, among birds of the burn, the Oregon ruffed grouse *Bonasa umbellus sabini,* sparrow hawk *Falco sparverius phalaena,* nighthawk *Chordeiles virginianus* ssp., Lewis woodpecker *Asyndesmus lewisi,* Gambel sparrow *Zonotrichia leucophrys gambeli,* golden-crowned sparrow *Zonotrichia coronata,* Townsend solitaire *Myadestes townsendi,* western robin *Planesticus migratorius propinquus,* mountain bluebird *Sialia currucoides,* and western bluebird *Sialia mexicana occidentalis;* and among the mammals the black bear *Ursus americanus,* red fox *Vulpes cascadensis,* various meadow mice *Microtus* sp., mountain beaver *Aplodontia rufa rainieri,* jumping mouse *Zapus trinotatus trinotatus,* two kinds of chipmunks *Eutamias townsendi cooperi* and *E. amoenus caurinus,* and the Columbian black-tailed deer *Odocoileus columbianus.* Bears, deer, and chipmunks are often particularly numerous.

Brush is, of course, a characteristic of burns, often occurring also on meadow borders and along stream courses. In addition to certain ones of the birds listed above, there are others which are characteristically brush-inhabiting, such as the Oregon towhee *Pipilo maculatus oregonus,* rusty song sparrow *Melospiza melodia morphna,* Lincoln sparrow *Melospiza lincolni,* fox sparrows *Passerella iliaca* ssps., lutescent warbler *Vermivora celata lutescens,* Tolmie warbler *Oporornis tolmiei,* and the golden pileolated warbler *Wilsonia pusilla chryseola.*

### *Habitats Characterized by Deficient Moisture or of a Rocky Type*

*Alpine Ridge and Pumice Slope.*—Above timberline in the intervals between glaciers and snowfields appear rocky ridges, the so-called cleavers, and more or less extensive pumice fields. With increase in altitude both flora and fauna quite naturally become less abundant, until finally, a little above 10,000 feet on Mount Rainier, practically all life ceases.[3] On the pumice fields and rocky ridges appear mountain phlox *Phlox diffusa,* mountain sorrel *Oxyria digyna,* Lyall lupine *Lupinus lyallii, Spraguea multiceps,* alpine buckwheat *Eriogonum pyrolaefolium coryphaeum, Hulsea nana, Polemonium elegans,*

[3] At least two mammals, the white-footed mouse, *Peromyscus maniculatus oreas,* and the little chipmunk, *Eutamias amoenus caurinus,* have been found near the summit of the mountain, altitude well over 14,000 feet. (See Taylor, 1920, p. 93.)

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golden aster *Erigeron aureus,* mountain aster *Oreostemma alpigena, Polygonum newberryi, Poa suksdorfii, Draba aureola,* and *Smelowskia ovalis.* Birds include the Rainier white-tailed ptarmigan *Lagopus leucurus rainierensis,* golden eagle *Aquila chrysaetos,* rosy finch *Leucosticte tephrocotis littoralis,* and pipit *Anthus rubescens.* One mammal, the mountain goat *Oreamnos montanus,* makes its home here. Several others range into the habitat, among them the red fox *Vulpes cascadensis,* Canada lynx *Lynx canadensis,* timber wolf *Canis gigas,* coyote *Canis latrans lestes,* black bear *Ursus americanus,* white-footed mouse *Peromyscus maniculatus oreas,* large-footed meadow mouse *Microtus richardsoni arvicoloides,* Cascade hoary marmot *Marmota caligata cascadensis,* and little chipmunk *Eutamias amoenus caurinus.*

*Rock-slide.*—Stupendous amphitheaters formed principally by the tearing away of frost-split fragments of rock by glaciers are a characteristic topographic feature on all sides of the mountain. Rock slides or taluses are the inevitable and necessary consequence of weathering in this region, and are conspicuous in the Hudsonian Zone between altitudes of 4,500 and 6,500 feet.

Certain plants and animals have become well adapted to life in the rock-slides, which furnish them with home and shelter. Among plants, *Phegopteris alpestris,* vine maple *Acer circinatum,* and mountain ash *Pyrus occidentalis* are often found on the rock-slides. One mammal, the cony *Ochotona fenisex brunnescens,* is found almost exclusively in this habitat, though several others are frequently observed in it, these including the marten *Martes caurina caurina,* Washington weasel *Mustela washingtoni,* Streator weasel *M. streatori,* white-footed mouse *Peromyscus maniculatus oreas,* western bushy-tailed woodrat *Neotoma cinerea occidentalis,* little chipmunk *Eutamias amoenus caurinus,* mantled ground squirrel *Callospermophilus lateralis saturatus,* and Cascade hoary marmot *Marmota caligata cascadensis.* The Rainier white-tailed ptarmigan *Lagopus leucurus rainierensis* spends much time on the rock-slides, although it is more characteristic of alpine ridge, glacier, and pumice slope.

*Glacier.*—It is difficult to decide just where to place the "Glacier" habitat, for though it is characterized by extreme moisture, this moisture is mostly unavailable, and the habitat is actually closely related, so far, at least, as its birds and mammals are concerned, to alpine ridge and pumice slope.

As is well known, several species of insects, chiefly members of the low order *Thysanura,* are found on the surface of the glaciers; worms of the genus *Mesenchytraeus* occur plentifully on the lower parts of the glaciers; and probably numerous microscopic plants are also to be found. The bacterium *Protococcus nivalis,* colonies of which make the patches of red snow, is conspicuous because of its color (Matthes, 1914, pp. 16–17). The pea fern *Cryptogramma acrostrichoides,* stone crop *Sedum divergens,* mountain alder *Alnus sinuata,* and *Collomia debilis* grow on the moraines in intimate relation to glaciers.

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No birds or mammals are exclusive inhabitants of the glacier habitat, but a number of them are occasionally found on the glaciers. These include the Rainier white-tailed ptarmigan *Lagopus leucurus rainierensis* and rosy finch *Leucosticte tephrocotis littoralis* among birds, and two kinds of weasels *Mustela washingtoni* and *M. streatori*, the marten *Martes caurina caurina*, timber wolf *Canis gigas*, coyote *Canis latrans lestes*, black bear *Ursus americanus*, mountain lemming mouse *Phenacomys orophilus olympicus*, and mountain goat *Oreamnos montanus* among mammals.

## Special Considerations

### The White River Area

White River, rising in Glacier Basin northeast of the mountain, trends in a general northeasterly direction until it leaves the Park at its extreme northeast corner. The broad basin drained by this river possesses several noteworthy peculiarities. The upper boundary of the Canadian Zone, in this region, is 500 feet higher than elsewhere about the mountain; the area is noticeably more arid than other parts of the Park; and there are differences both in fauna and flora. The trees on the northeast side of the mountain do not attain the huge dimensions of those of the west and southwest. *Picea engelmanni* and *Ceanothus velutinus* appear for the first time, and *Pinus contorta* and *P. albicaulis* become far more abundant than elsewhere. Among mammals *Callospermophilus lateralis saturatus, Marmota caligata cascadensis,* and apparently *Eutamias amoenus caurinus* are more numerous. *Thomomys douglasii shawi* occurs on the east side of the Park only, from Cowlitz Ridge to Grand Park. Among birds *Nucifraga columbiana* is more common in this section than elsewhere, and *Spizella passerina arizonae* was here recorded for the first time.

Areas of obvious aridity, as Yakima and Grand Parks, are conspicuous on the northeast side of the mountain. One day during the first week in August, 1919, as the writer stood on Panhandle Gap (altitude 7,300 feet) with a great area of Mount Rainier Park in full view to the north, east, and south, a heavy fog was observed obscuring the Longmire country, Stevens Canyon, and, in fact, all the region to the south and west; while Summerland, White River, and the country to the north and east were free from fog or were shadowed by scattered cloud masses only. Subsequent evidence indicated that there is a real and probably not inconsiderable climatic difference between the areas which on that occasion were fog-covered and those where the sun was shining.

The relative aridity of the northeast side of Mount Rainier can apparently be accounted for by the direction of the winds in the region. According to J. B. Flett, Senior Park Ranger and Cooperative Weather Observer, at Longmire, Mount Rainier, Washington, the prevailing direction of the wind is

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southwest, nine tenths of all the storms coming from that direction. While weather records from the east and northeast sides of Mount Rainier are lacking, we can safely conclude that there is far less precipitation there than on the west and southwest slopes. The order of difference which might be expected may perhaps be fairly assumed from the consideration of a near-by region. Clearwater, Jefferson County, Washington, lying southwest of the Olympic Mountains, received, between the years 1898 and 1907, inclusive, a mean annual precipitation of 127.90 inches; while Seattle, lying east of the Olympics, received, between the years 1892 and 1913, inclusive, a mean annual precipitation of but 34.36 inches (Salisbury, 1915, p. 5). There is, then, little doubt that considerably more snow falls on the southwest slopes of Mount Rainier than on the northeast. If this is the case, one would expect the various zonal boundaries to be somewhat higher on the northeast than on the southwest, for the snow would disappear at an earlier date and the warm growing season would be prolonged.

The direction of the prevailing winds probably accounts also for the presence in the northeast part of the Rainier Park of a greater amount of volcanic ash soil than elsewhere about the mountain. This soil is of an extremely porous character and does not hold moisture, consequently wherever it appears the country is likely to have a dry aspect. Whatever may be the cause, it is a fact that Yakima Park, the Sourdough Mountain district, and the Grand Park region, all of which lie northeast of the mountain, are the most arid-appearing portions of the entire Rainier area.

## Timberline on Mount Rainier

The extreme limit of tree growth on Mount Rainier is 7,600 feet above sea level (Allen, 1916, p. 3), but trees seldom reach this altitude. As Piper has noted (1906, p. 62) timberline extends to a much higher altitude on the ridges than in the draws between, there being more than 2,000 feet difference on Mount Rainier. The average altitude of timberline on the mountain is 6,500 feet.

To one accustomed to Rocky Mountain or Sierran conditions this will seem surprisingly low, especially in view of the fact that Mount Rainier has a warm humid climate. Even on the east slopes of the Cascade Mountains of Washington, where the climatic extremes are considerably more severe, timberline averages about a thousand feet higher.

In their recent paper on the plants and animals of Mount Marcy, New York, Adams, Burns, Hankinson, Moore, and Taylor suggest that effective temperatures, wind, and depth of snow are the most important factors causing timberline on mountains (1920, p. 286). While it is altogether likely that these factors, and possibly others, have an effect on Mount Rainier, it is not improbable that the excessive snowfall on the mountain is the most important of them all (see Allen, 1916, p. 3).

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The winter storms frequently begin as early as September, and the steadily accumulating snow lasts through until the following July. Timberline trees are subjected to a stress and strain of the severest character. The congealing of the moist snow on their branches frequently weights them down so that their branches are actually broken off, and sometimes the entire tree is laid low. The comparatively moderate winter temperature probably has an effect here, the alternate freezing and thawing doubtless being more difficult to withstand than is a considerably lower temperature.

FIG. 1. Trees in winter at 5,800 feet altitude near timber line on Mount Rainier. One tree (on left) has been broken down. Photograph taken January 20, 1920, by J. B. Flett.

Although greater extremes of temperature are undoubtedly registered on the east slopes of the Cascades in Washington, the snowfall is not nearly so heavy, and the trees run up the mountain sides for a thousand feet more of vertical altitude.

Furthermore, that depth of snow, rather than effective temperature or wind, is the factor of preponderant influence in determining timberline on Mount Rainier is indicated by the fact that on the ridges, which receive the full force of the wind, and some of which are undoubtedly colder than the draws between, the trees go considerably higher than they do in the draws.

The boundaries of all the life zones tend to be lower on Mount Rainier

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than on the east slopes of the Cascades. This may be because the sum total of heat units necessary for floral growth and development is less at a given altitude on the west than on the east side. It is unlikely that depth of snow would be of any great importance in determining zonal boundaries below timberline.

In a less humid environment than that of Mount Rainier, as on the east slopes of the Cascades, in the Sierra Nevada or the Rocky Mountains, there would ordinarily be a difference of at least 500 feet (sometimes much more) in the altitude of timberline on north and south slopes. On Mount Rainier this difference is so small that in many localities it is scarcely appreciable.[4] The effects of humidity through the Rainier region seem to so dominate that the effects of temperature, which would otherwise be clearly registered on north and south slopes, are minimized.

## Distributional Problems

### Composition of Bird and Mammal Communities and Direction of Ingression

The direction of ingression of 33 species of mammals out of the 55[5] found in the Park, and of 30 birds out of 102, can be tentatively stated.

Taking the mammals first, 18 species quite certainly entered Mount Rainier from the east and 15 from the west. Lists of these species follow.[6]

| From the Coastal Strip West of Mount Rainier | From the Cascade Mountains East of Mount Rainier |
|---|---|
| *Scapanus townsendii* | *Neosorex navigator navigator* |
| *Scapanus orarius* | *Canis latrans lestes* |
| *Neurotrichus gibbsii gibbsii* | *Vulpes cascadensis* |
| *Neosorex bendirii bendirii* | *Lynx canadensis* |
| *Sorex obscurus setosus* | *Gulo luscus* |
| *Sorex trowbridgii* | *Martes caurina caurina* |
| *Spilogale phenax olympica* | *Martes pennanti pacifica* |
| *Mustela streatori* | *Microtus richardsoni arvicoloides* |
| *Microtus oregoni* | *Microtus mordax mordax* |

[4] South-facing slopes are, however, more regularly and heavily timbered than north-facing, due apparently, to the fact that snow banks on the north-facing slopes last longer than on south-facing slopes; then, too, alternate thawing and freezing on south slopes would make more water available over a longer period than on north slopes.

[5] Some of the species cannot be classified as to direction of ingression, either because they are so wide-ranging that they cannot be said to have entered the Park from any one direction, or because their exact systematic status is uncertain.

[6] Additional information is likely to modify these lists, which, in the present state of knowledge, must be regarded as tentative. The data presented do, however, suffice, in the writer's opinion, to justify the general conclusions set forth.

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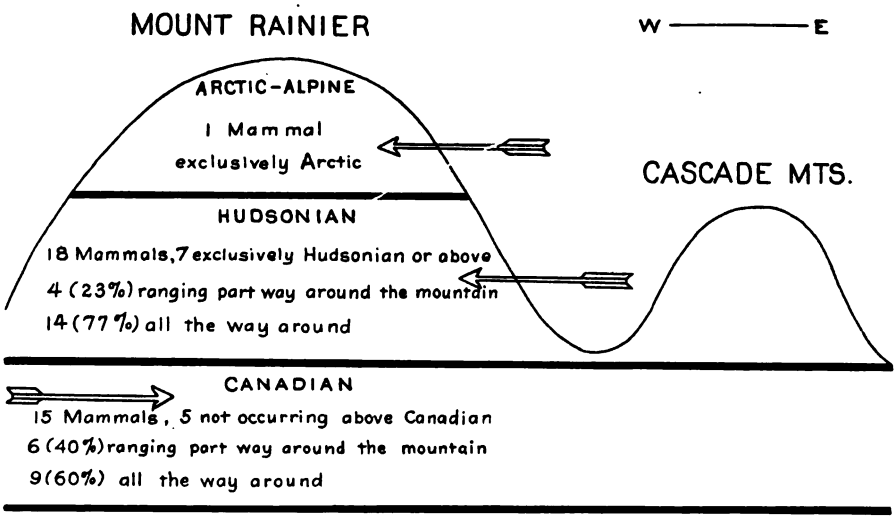
*Zapus trinotatus trinotatus*
*Aplodontia rufa rainieri*
*Eutamias townsendi cooperi*
*Sciurus douglasii douglasii*
*Lepus washingtonii washingtonii*
*Odocoileus columbianus columbianus*
*Evotomys gapperi saturatus*
*Phenacomys orophilus olympicus*
*Thomomys douglasii shawi*
*Callospermophilus lateralis saturatus*
*Glaucomys sabrinus fuliginosus*
*Eutamias amoenus caurinus*
*Ochotona fenisex brunnescens*
*Marmota caligata cascadensis*
*Oreamnos montanus montanus*

Mammals ingressing from the west are all derived from or referable to the Canadian or Humid Transition zones of the Vancouver Strip of Piper (1906, p. 40). All occur in the Canadian Zone on Mount Rainier, and all but 5 (*Neurotrichus gibbsii gibbsii, Neosorex bendirii bendirii, Sorex trowbridgii, Spilogale phenax olympica,* and *Lepus washingtonii washingtonii*) have penetrated the Hudsonian Zone. Mammals ingressing from the east are principally derived from the Hudsonian Zone of the high Cascade Mountains. All are known to occur in the Hudsonian Zone on Mount Rainier, and 7 are not known to occur below the Hudsonian Zone. These are *Vulpes cascadensis, Gulo luscus, Phenacomys orophilus olympicus, Thomomys douglasii shawi, Eutamias amoenus caurinus, Marmota caligata cascadensis,* and *Oreamnos montanus montanus.*




DERIVATION OF MAMMALS ON MOUNT RAINIER

FIG. 2. Diagrammatic cross section of Mount Rainier and the Cascade Mts. from east to west, showing the direction from which the mammals in each zone have come. (Arrows indicate direction of invasion.)

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Treating the birds similarly we find that of the species which may be classified in respect to direction of ingression 12 come from the coastal strip to the west, and 18 from the Cascade Mountains to the east. The lists follow:

| From the Coastal Strip West of Mount Rainier | From the Cascade Mountains East of Mount Rainier |
|---|---|
| *Ardea herodias fannini* | *Dendragapus obscurus fuliginosus* |
| *Lophortyx californica californica* | *Lagopus leucurus rainierensis* |
| *Bonasa umbellus sabini* | *Pica pica hudsonia* |
| *Empidonax difficilis* | *Stellula calliope* |
| *Cyanocitta stelleri stelleri* | *Dryobates villosus orius* (?) |
| *Melospiza melodia morphna* | *Nucifraga columbiana* |
| *Thryomanes bewicki calophonus* | *Carpodacus cassini* |
| *Nannus hiemalis pacificus* | *Loxia leucoptera* |
| *Penthestes rufescens rufescens* | *Leucosticte tephrocotis littoralis* |
| *Regulus satrapa olivaceus* | *Spizella passerina arizonae* |
| *Hylocichla ustulata ustulata* | *Melospiza lincolni lincolni* |
| *Ixoreus naevius naevius* | *Passerella iliaca schistacea* |
| | *Anthus rubescens* |
| | *Sitta canadensis* |
| | *Penthestes gambeli gambeli* |
| | *Myadestes townsendi* |
| | *Hylocichla guttata sequoiensis* |
| | *Sialia currucoides* |

Of the 12 birds which have come in from the west, 6 are confined to the Canadian or a lower zone. These are *Ardea herodias fannini, Lophortyx californica californica, Bonasa umbellus sabini, Empidonax difficilis, Thryomanes bewicki calophonus, Hylocichla ustulata ustulata.* The others range into the Hudsonian Zone to the limit of trees, though several appear to find optimum conditions in the Canadian Zone. No Alpine-Arctic or purely Hudsonian species appear to have ingressed from the west.

Each of the 18 species derived from the Cascade Mountains to the east, except three which are principally Arctic-Alpine (*Lagopus leucurus rainierensis, Leucosticte tephrocotis littoralis,* and *Anthus rubescens*), occurs commonly in the Hudsonian Zone. One of the species, *Sitta canadensis,* has apparently found the most favorable conditions in the Canadian Zone. Most of the others find optimum conditions in the Hudsonian Zone. Of the birds ingressing from the east there are 4 which are seldom or never found below the Hudsonian Zone, including the three Arctic-Alpine forms just mentioned, and *Nucifraga columbiana* in addition.

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It thus appears that the classifiable species characteristic of the Hudsonian Zone have come from the Hudsonian of the Cascade Mountains to the east, while the classifiable species characteristic of the lower zones have come from the west. It is well known that in general the invisible barriers to geographical distribution, as temperature and humidity, are often more potent than topographic barriers. These invisible barriers certainly have had much to do

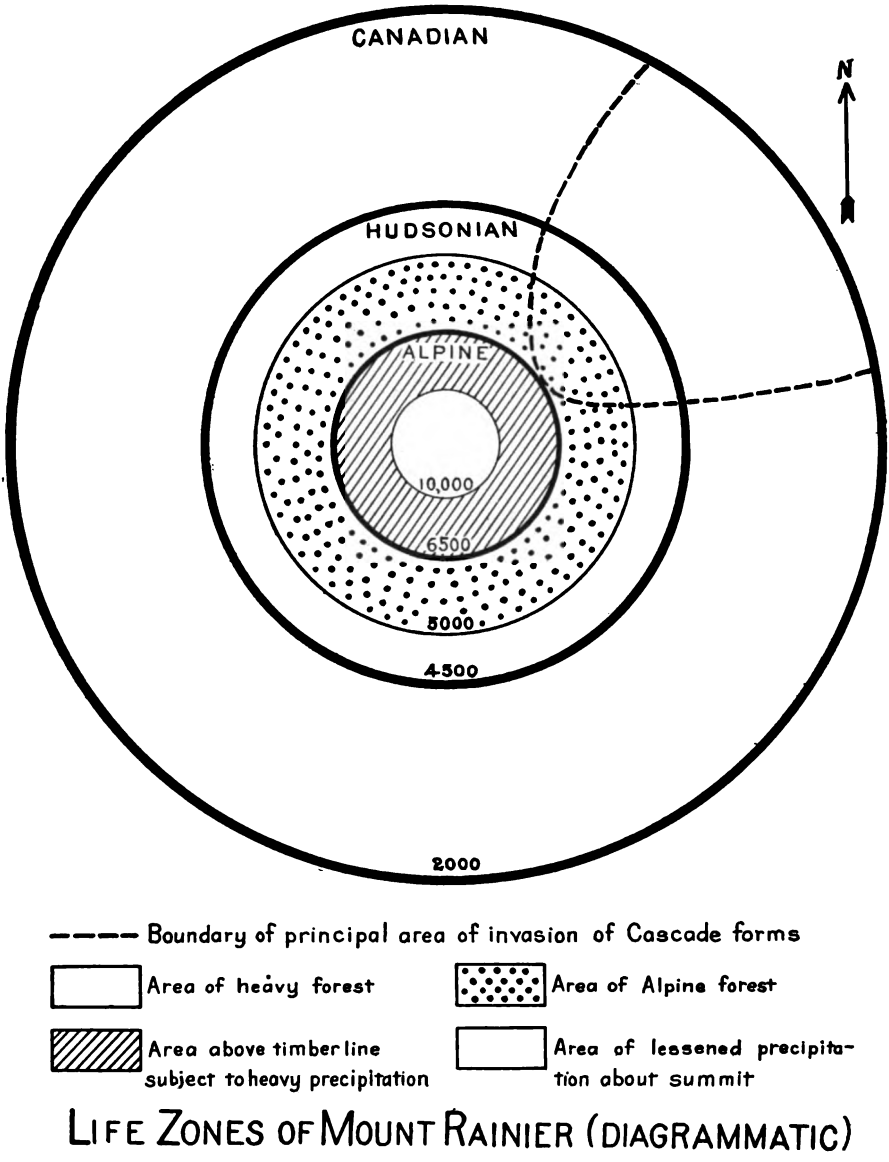


FIG. 3. Life zones and timber belts of Mount Rainier, showing the area of principal invasion of birds and mammals from the Cascade Mountains.

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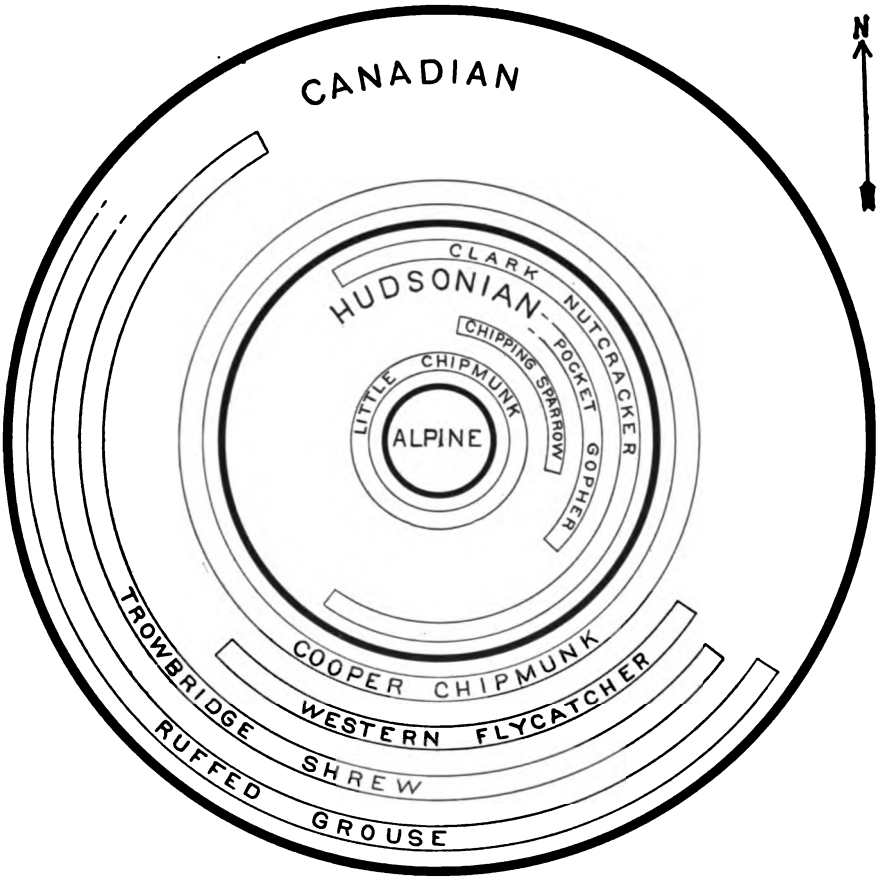
with the distribution of the birds and mammals of Mount Rainier. Incidentally the usefulness of the life zone concept in elucidating the composition of communities is demonstrated, even in a region where the effects of humidity are pervasive and almost preponderant.

## Distribution about the Mountain of Birds and Mammals from East and West

The distribution of the species within a given zone is not uniform about the mountain. For example, of the 15 mammals ingressing from the west, there appear to be only 9 which are to be found all the way around the mountain.[7] The other species, 6 in number, are found on the west side, but




DISTRIBUTIONAL PROBLEMS ON MT RAINIER

Fig. 4. Diagrammatic representation of the distribution of certain birds and mammals around Mount Rainier.

[7] The ranges of some of the others might, of course, be extended by further investigation.

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range to different distances about the mountain to the east. The latter include *Scapanus townsendi, Neurotrichus gibbsii gibbsii, Sorex trowbridgii, Neosorex bendirii bendirii, Spilogale phenax olympica,* and *Lepus washingtonii washingtonii.* Of the 12 birds which have come from the west, only 7 are found all the way around the mountain, the other 5 (*Ardea herodias fannini, Lophortyx californica californica, Bonasa umbellus sabini, Empidonax difficilis, Thryomanes bewicki calophonus*) ranging only part way around.

Of the 18 mammals which have ingressed from the Cascades, all but 4 (*Neosorex navigator navigator, Microtus mordax mordax, Thomomys douglasii shawi, Callospermophilus lateralis saturatus*) have found their way entirely around the mountain. Of the 18 birds which have come in from the Cascades, all but 3 have found their way all about the mountain, the 3 being *Nucifraga columbiana, Spizella passerina arizonae, Penthestes gambeli gambeli.*

Of the birds and mammals from the west, 16 are found all around the mountain and 11 part way; of those from the east, 29 are found all around the mountain and 7 part way. It seems obvious that it has been possible more often for species ingressing from the east to extend their geographic range about the mountain than for those derived from the west. This is probably because the Hudsonian Zone environment, including climate, vegetation, and topography, is more uniform than the Canadian Zone environment. The actual distance around the mountain is greater in the Canadian Zone, but the distances are short at the longest, and it seems unlikely that the comparative distribution of the species concerned offers any valid suggestion as to the relative times of ingression or the relative rates of range extension.

Data regarding ingression of mammals and birds and their distribution about the mountain may be summarized as follows:

*Mammals*

| | | |
|---|---|---|
| Species ingressing from the Cascade Mountains east of Mount Rainier .... | 18 | |
| (All occur in the Hudsonian Zone and 7 do not occur below it) | | |
| Species ingressing from the coast strip, west of Mount Rainier ..... | 15 | |
| (All occur in the Canadian Zone and 5 do not occur above it) | | |
| Species ingressing from the east, found all the way around the mountain .. | 14 | 77% + |
| Species ingressing from the east, found part way only around the mountain | 4 | 22% + |
| Species ingressing from the west, found all the way around the mountain .. | 9 | 60% |
| Species ingressing from the west, found part way around the mountain .... | 6 | 40% |

*Birds*

| | |
|---|---|
| Species ingressing from the Cascade Mountains east of Mount Rainier .... | 18 |
| (All occur in the Hudsonian Zone and 4 do not occur below it) | |
| Species ingressing from the Coast Strip west of Mount Rainier ..... | 12 |
| (All occur in the Canadian Zone and 6 do not occur above it) | |

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| | | |
|---|---|---|
| Species ingressing from the east, found all the way around the mountain ... | 15 | 83% + |
| Species ingressing from the west, found part way only around the mountain | 3 | 16% + |
| Species ingressing from the west, found all the way around the mountain .. | 7 | 58% + |
| Species ingressing from the west, found part way only around the mountain | 5 | 41% + |

### *Derivation of Zonal Assemblages*

1. All classifiable species of both birds and mammals characteristic of the Arctic-Alpine Zone are derived from the Cascade Mountains to the east.

2. All classifiable species, both birds and mammals, characteristic of the Hudsonian Zone are derived from the Cascade Mountains.

3. All classifiable species, both birds and mammals, characteristic of the Canadian Zone are derived from the Coast strip.

4. All classifiable species, both birds and mammals, characteristic of the Transition Zone are derived from the Coast strip.

## Summary

1. Mount Rainier is a massive eminence, chiefly basaltic in character, with a warm humid climate and an extremely heavy snowfall. The climatic conditions result in the formation of numerous glaciers. Differences in precipitation on the different sides of the mountain exercise an important influence on the distribution of its birds, mammals, and plants.

2. The *life zone,* mapped on broad lines with *temperature* as the basic factor, and the *habitat* with its *association,* determined chiefly on *water relations,* are relied on to show the distribution of plant and animal life on the mountain.

3. Four life zones are represented, the Transition, Canadian, Hudsonian, and Arctic-Alpine. In general, the Transition Zone includes areas in the southeastern part of the Park below 3,000 feet; the Canadian, the heavily timbered area between 2,000 and 4,500–5,000 feet; the Hudsonian, the subalpine meadow country between 4,500–5,000 and 6,500 feet; the Arctic-Alpine, the region above timberline, 6,500 feet and over.

4. The habitats are roughly divisible into three groups: those characterized by extreme moisture, including stream, stream-border, lake, lake-shore, and swamp; those characterized by moderate moisture, including meadow, forest, and burn; and those characterized by deficient moisture or of a rocky type, including alpine ridge, pumice slope, rock-slide, and, tentatively, glacier.

5. The White River region, in the northeastern portion of the Park, possesses several peculiarities: the upper boundary of the Canadian Zone is 500 feet higher in this region than elsewhere in the Park; the White River area is noticeably drier than other parts of the Park; and there are peculiarities in the fauna and flora of the region. These peculiarities probably arise partly or largely from differences in climate induced by the topography of the Rainier region as related to the prevailing southwest winds.

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6. Depth of snow seems to be more important than effective temperatures, winds, or other factors in causing timberline on Mount Rainier. The usual effects of temperature in determining the altitude of timberline on north and south slopes are minimized, apparently through the pervasive effects of humidity about the mountain.

7. It has been possible to classify tentatively 63 species of mammals and birds (33 mammals, 30 birds) as to direction of ingression; in general, the mammals and birds of the higher levels on the mountain are derived from the Cascade Mountains east of Mount Rainier, while those of lower levels are derived from the coast strip to the west. Species ingressing from the east have been more successful in extending their ranges about the mountain than those from the west, probably because of the more uniform environment in the higher zones.

The writer is indebted to J. B. Flett, of the National Park Service, Longmire, Mount Rainier National Park, Washington, for generous aid in compiling plant lists and in furnishing photographs; to C. V. Piper, of the Bureau of Plant Industry, Washington, D. C., for correcting plant names used; to Mrs. Jane S. Elliott, of the Bureau of Biological Survey, Washington, D. C., for line drawings utilized; and to E. A. Goldman, E. A. Preble, Hartley H. T. Jackson, and George G. Cantwell, of the Bureau of Biological Survey, for valued advice and helpful suggestions.

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# RELATION OF HARDPAN TO ROOT PENETRATION IN THE GREAT PLAINS

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During the excavation of root systems of native and crop plants throughout the Great Plains region during the past five years (Weaver, 1919, 1920, 1922) contact has been made in more than thirty fields with the so-called hardpan. Such a layer of soil underlies much of this area of low rainfall, at depths varying from 15 inches to 3 feet. It varies from 8 inches to over 1.5 feet in thickness. In connection with studies on the physical and chemical composition of the soils and their seasonal water-content under natural and cropped conditions, a more detailed study has been made of the soil in this hardened layer. The major portion of this work was done at Burlington, Colorado, a station selected as being typically representative of High Plains conditions, but analyses of hardpan from Flagler, Colorado, and Colby, Kansas, were also made.

## The Hardpan

Mechanical and chemical analyses of the soils at Burlington are given in Tables 1 and 2. These represent the several foot sections to a depth of six feet, except in the first foot, where samples were taken to depths of six and twelve inches, respectively. The samples from Flagler and Colby were obtained from the hardpan layer at depths of approximately 1.3 to 2.1 and 1.9 to 2.6 feet, respectively. At Flagler the field had been broken only one year, at Colby for a number of years. The cropped area at Burlington was on land broken only 3 years. Here a well-formed hardpan occurred at a depth of about 2 feet. The change in soil structure was quite distinct, the harder layer continuing to a depth of 4 feet, where it gave way to a loess-like soil very loose and powdery in structure. Hence in Tables 1 and 2 the first three samples are of soil above the hardpan, the next two in the hardpan, while the last two are from the soil below it.

An examination of Tables 1 and 2 shows that the hardpan at Flagler and also that at Colby appears to be due solely to the calcareous nature of the soil. The former contains a relatively low percentage of clay and at the same time more inorganic carbonate along with calcium oxide than any one of the Burlington samples. The Colby sample is higher in clay content, but holds nearly twice the amount of carbonate compounds. At Burlington the case is different. Here calcareousness alone does not account for the condition. Although the carbonates increase with depth, they do not reach a concentration sufficient to bring about the hardening of the soil, unless their effect is supple-



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mented by other agencies. Furthermore, the carbonates are more abundant below the hardpan than in it.

TABLE 1. *Mechanical analyses and moisture constants of soils*

| Burlington, Colo. | Coarse gravel | Fine gravel | Coarse sand | Medium sand | Fine sand | Very fine sand | Total sand | Silt | Clay | Hygroscopic coefficient | Moisture equivalent |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Feet | | | | | | | | | | | |
| 0.0 to 0.5 | 0.0 | 0.0 | 0.0 | 0.2 | 2.5 | 48.6 | 51.3 | 33.4 | 15.3 | 10.7 | 24.9 |
| 0.5 to 1.0 | 0.0 | 0.0 | 0.0 | 0.2 | 2.1 | 49.1 | 51.4 | 32.5 | 16.1 | 10.8 | 25.2 |
| 1 to 2 | 0.0 | 0.0 | 0.0 | 0.2 | 1.8 | 46.7 | 48.7 | 32.0 | 19.3 | 11.6 | 26.6 |
| 2 to 3 | 0.0 | 0.0 | 0.0 | 0.1 | 1.5 | 45.5 | 47.1 | 31.0 | 21.9 | 12.1 | 27.3 |
| 3 to 4 | 0.0 | 0.0 | 0.0 | 0.1 | 0.9 | 42.2 | 43.2 | 34.1 | 22.7 | 12.0 | 28.2 |
| 4 to 5 | 0.0 | 0.0 | 0.0 | 0.1 | 0.8 | 52.6 | 53.5 | 31.3 | 15.2 | 10.9 | 24.1 |
| 5 to 6 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 56.8 | 57.8 | 28.8 | 13.4 | 10.0 | 22.1 |
| Flagler, Colo. | 0.0 | 0.0 | 0.0 | 0.1 | 0.9 | 44.3 | 45.3 | 40.1 | 14.6 | 10.9 | 27.6 |
| Colby, Kans. | 0.0 | 0.0 | 4.0 | 2.7 | 3.4 | 38.1 | 48.2 | 29.6 | 22.2 | 10.2 | 25.0 |

TABLE 2. *Chemical analyses of soils (total)*

| Burlington, Colo. | $SiO_2$ | Fe, Al, Ti Oxides | CaO | MgO | $CO_2$ | $P_2O_5$ | Nitrogen | Volatile matter | Organic matter | Water of hydration |
|---|---|---|---|---|---|---|---|---|---|---|
| Feet | | | | | | | | | | |
| 0.0 to 0.5 | ..... | ..... | .... | .... | 0.03 | 0.189 | 0.184 | 4.67 | 3.14 | 1.53 |
| 0.5 to 1.0 | ..... | ..... | .... | .... | 0.30 | 0.504 | 0.130 | 3.13 | 2.05 | 1.08 |
| 1 to 2 | ..... | ..... | .... | .... | 1.71 | 0.428 | 0.101 | 3.11 | 1.56 | 1.55 |
| 2 to 3 | ..... | ..... | .... | .... | 2.09 | 0.406 | 0.086 | 3.34 | 1.58 | 1.76 |
| 3 to 4 | 69.26 | 16.25 | 5.30 | 0.88 | 2.59 | 0.525 | 0.084 | 2.84 | 1.41 | 1.43 |
| 4 to 5 | 66.68 | 16.48 | 5.51 | 0.92 | 2.99 | 0.169 | 0.041 | 1.60 | 0.50 | 1.10 |
| 5 to 6 | 67.29 | 15.39 | 5.48 | 0.91 | 3.28 | 0.161 | 0.032 | 1.14 | 0.45 | 0.69 |
| Flagler, Colo. | 66.64 | 15.98 | 5.97 | 0.99 | 3.45 | 0.380 | 0.054 | 1.19 | 0.61 | 0.58 |
| Colby, Kans. | 66.22 | 13.70 | 9.60 | 0.89 | 6.80 | 0.403 | 0.053 | 0.48 | 0.62 | −0.14 |

Table 1 shows a gradual increase in the percentage of clay from 15.3 percent in the first six inches of soil to 22.7 percent in the fourth foot, with a corresponding decrease in the amount of very fine sand. This means that there is a transition from a very fine sandy loam in the upper foot of soil to a clay loam in the region of the second to the fourth foot. A break comes at 4 feet, below which level the texture is again that of a very fine sandy loam. The hygroscopic coefficients and moisture equivalents consistently follow these differences in texture.

The clay content even in the hardpan is not outstandingly high. Many soils of easy tilth in more humid regions have much more clay. Hence the

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climatic factors, especially precipitation, on the Great Plains must be considered.

The normal annual precipitation at Burlington is 17 inches, of which by far the greater part falls during the spring and summer months. However, as is shown in Table 3 and confirmed elsewhere (Shantz, 1911), the water that actually penetrates deeper than 1.5 to 2 feet falls in the spring, when evaporation is relatively low and crops (now rooted entirely in shallow levels) are not making heavy demands upon the supply. During this period (April to June) the water may penetrate into the hardpan layer to some extent. When this occurs the hardpan softens and disappears as far as the wetting proceeds. Later, when drought conditions prevail, it dries out again and hardens as before. Table 3 indicates the water-content in excess of the hygroscopic coefficient (approximately the available water—*cf.* Weaver, 1920, p. 28) at the different levels for the growing seasons of 1920 and 1921, both seasons having a total precipitation somewhat above the normal. While many of the figures show a percentage below the hygroscopic coefficient, this is probably due in the surface soils to direct evaporation and elsewhere to local variations in the soil samples in regard to their relative amounts of sand and clay. Computations were made on the basis of the hygroscopic coefficient of a single carefully selected composite sample from each of the several levels (*cf.* Shantz, 1911, p. 30).

TABLE 3. *Water-content in excess of hygroscopic coefficient, Burlington, Colorado*

| Date | 0.0 to 0.5 ft. | | 0.5 to 1.0 ft. | | 1 to 2 ft. | | 2 to 3 ft. | | 3 to 4 ft. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Sod | Field | Sod | Field | Sod | Field | Sod | Field | Sod | Field |
| 1920 | | | | | | | | | | |
| Apr. 15 | 16.7 | 22.0 | 13.7 | 10.5 | 11.1 | 0.5 | 4.9 | −0.1 | 1.8 | −0.4 |
| June 3 | 2.3 | 5.3 | 5.2 | 6.4 | 7.3 | 3.1 | 6.9 | 5.1 | 2.9 | −0.6 |
| June 12 | −1.8 | 0.4 | −0.1 | 3.8 | 2.8 | 1.2 | ..... | ..... | ..... | ..... |
| June 25 | 7.4 | 6.4 | 2.5 | 1.7 | 1.8 | 0.8 | 1.4 | 2.7 | −2.5 | 1.6 |
| July 2 | −1.6 | −2.0 | −0.5 | −1.1 | 0.0 | 0.0 | ..... | ..... | ..... | ..... |
| July 8 | −2.9 | −2.0 | −1.3 | −0.4 | −2.2 | −1.4 | ..... | 0.7 | ..... | 1.8 |
| July 20 | −0.7 | 0.5 | −2.7 | −2.6 | −1.7 | −2.8 | 2.5 | −0.5 | −0.6 | 2.0 |
| Aug. 5 | 4.6 | 4.4 | 2.7 | 0.0 | −2.7 | 1.3 | −0.6 | 0.0 | −3.1 | −1.9 |
| Aug. 19 | −3.1 | ..... | −3.1 | ..... | −0.5 | ..... | ..... | ..... | ..... | ..... |
| Aug. 24 | −0.8 | −0.7 | −2.1 | −0.9 | −1.9 | −2.2 | −0.6 | 2.5 | −1.4 | −1.8 |
| 1921 | | | | | | | | | | |
| April 30 | 9.6 | 11.2 | 10.7 | 9.7 | 8.6 | 8.8 | 0.0 | 2.4 | 1.3 | 0.9 |
| May 20 | 6.4 | 6.6 | 5.6 | 7.4 | 4.7 | 3.5 | −0.7 | −0.7 | −2.2 | 0.2 |
| June 10 | 10.3 | 2.7 | 0.0 | 1.9 | 0.7 | 0.3 | −0.5 | −0.4 | −0.6 | −0.2 |
| June 30 | −2.6 | −2.6 | −1.6 | −1.9 | −1.5 | −2.1 | −1.0 | −1.0 | −1.3 | −1.3 |
| July 17 | −1.0 | ..... | −1.0 | ..... | −3.6 | ..... | ..... | ..... | ..... | ..... |
| July 24 | −3.5 | ..... | −2.2 | ..... | −3.4 | ..... | −1.8 | ..... | −0.4 | ..... |
| Aug. 8 | 2.0 | ..... | −0.7 | ..... | −2.1 | ..... | −0.3 | ..... | −1.0 | ..... |
| Aug. 17 | 16.9 | ..... | 11.7 | ..... | −2.4 | ..... | −2.0 | ..... | ..... | ..... |
| Aug. 29 | −0.3 | ..... | 0.5 | ..... | −2.1 | ..... | −0.4 | ..... | −1.0 | ..... |

From these data it is clear that the hardpan layer in general and its base in particular marked the limit of maximum penetration of rainfall. Shantz's

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findings (1911) and also those of Briggs and Shantz (1912) corroborate this conclusion.

Under these conditions of water penetration, the concentration of colloidal clay and carbonates in the subsoil is sufficient to give rise to a hardpan—*i.e.*, a much more compact stratum of soil relative to that above or below it—upon its becoming so completely dried out. The cementing power of ultra-clay when the material is dry is very striking, quite exceeding that of Portland cement, as has been demonstrated by Moore *et al.* (1921). Jensen (1918) found that "plowsole" in the citrus groves of southern California contained a higher percentage of inorganic colloid suspension than the soil mulch, and usually a higher percentage than the subsoil. Table 2 shows that the water of hydration in the soils at Burlington, obtained by subtracting the organic matter from the volatile matter, is highest in the hardpan layer and falls off remarkably below it.

## Root Distribution of Native Plants

Root distribution of native vegetation has been determined at several widely separated stations in Colorado. Not only the dominant grasses, but numerous subdominants, including non-grassy species, have been examined. About 5 miles northwest of Sterling, Colorado, the following species were studied: buffalo grass *Bulbilis dactyloides*, grama *Bouteloua gracilis*, wire grass *Aristida purpurea*, Texas crab grass *Schedonnardus paniculatus*, brown-weed *Gutierrezia sarothrae*, and a cactus *Opuntia polyacantha*. The open mats of buffalo and grama grass indicate a low water-content. Much of the 15 inches of annual precipitation is lost by run-off from the very compact fine-sandy loam, which is underlaid at a depth of 2 feet with a well-defined hard-pan about 8 inches thick.

*Bulbilis dactyloides*, a dominant of the short-grass plains and a species with a very wide distribution, has been excavated in many places. While soil type and water relations have some effect upon the extent of the lateral distribution of rootlets in the surface soil, this being much more pronounced in drier soils, the depth of penetration remains quite uniform, about 5 to 7 feet. At Sterling the fine, well-branched, fibrous roots penetrated the hard-pan and extended into a very dry layer of gravel and small pebbles mixed with sand, many roots reaching a depth of over 5.5 feet.

The roots of *Bouteloua gracilis* are similar in fineness and degree of branching to those of *Bulbilis* and, like those of the latter, they spread widely, 1.5 feet or more on all sides of the plant, in dry soils. They normally reach a working depth (*i.e.*, a level to which many roots penetrate and to which depth considerable absorption occurs) of about 3 feet and have a maximum penetration of at least 4 feet. At Sterling the soil was quite filled with the roots of this dominant to a depth of 2.5 feet; they were fairly abundant to 3.2 feet, while some extended a foot deeper.

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*Aristida purpurea* characterizes large areas of grassland throughout the Great Plains, especially where the soil is slightly sandy or where overgrazing or other disturbance has given it a foothold in competition with buffalo and grama. Typically the coarse fibrous roots spread laterally 5 to 8 inches, and, unlike the preceding short-grasses, branch but little in the surface 4 inches of

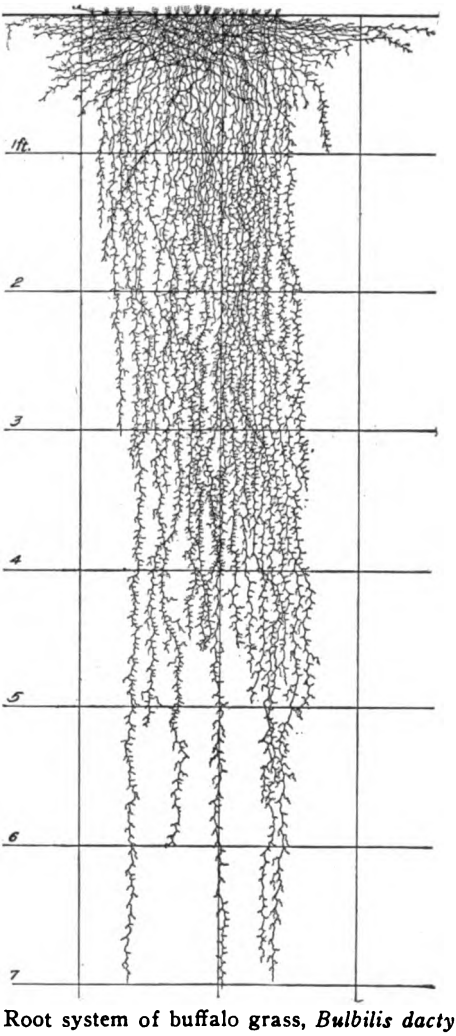


FIG. 1. Root system of buffalo grass, *Bulbilis dactyloides.*

soil. However, its working depth is about 2.5 feet and the maximum penetration 3 or 4 feet. In the sod at Sterling the bunches, which were rather small, had a lateral spread of roots of 7 inches, but none penetrated more than 0.3 foot into the hardpan.

The annual or sometimes short-lived perennial, *Schedonnardus panicu-*

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*latus,* is nearly always present in small numbers in the short-grass sod. It is an excellent indicator of overgrazing or other disturbance. The root habit is much like that of *Aristida,* but the depth of penetration is only about two feet.

*Gutierrezia sarothrae* is a perennial half-shrub which forms societies throughout the plains region. Rather small specimens occurred at Sterling. The woody tap roots were 4 to 8 mm. in diameter. These were furnished with abundant laterals, many of which spread 0.5 to 1.5 feet in the surface 3 or 4 inches of soil before ending or turning downward. Most of the branches ended in the third or fourth foot of soil and none were traced to a greater depth than 5 feet. In more moist areas greater lateral spread and deeper penetration (6.5 feet) have been determined.

*Opuntia polyacantha* is a plant of common occurrence in short-grass lands and frequently of great abundance in over-grazed areas. Like many other cacti, the root system consists of two rather distinct parts—a few vertically descending roots and many shallow ones which spread widely in the surface 3 or 4 inches of soil. The four or five roots of each plant which descended vertically were only fairly well branched and did not extend beyond 2 feet in depth. The profusely branched shallow roots (14 to 24 per plant) spread laterally to distances of 1 to 5.5 feet.

Thus among the six species examined at this station four had a working level below or well within the hardpan layer, while two penetrated into it slightly or not at all, since their root systems are normally developed in the first two feet of soil.

At Yuma, Colorado, the soil consists of a brown fine-sandy loam, which is very hard when dry and breaks out in lumps, showing more or less of a columnar structure. It is underlaid, where the roots were excavated, at a depth of 2.8 feet by a well-formed hardpan which was 8 to 10 inches thick. Below this layer the loess was mellow and at 7 feet in depth of an ashy consistency. The roots of buffalo grass were found to have a working depth of 5 feet and a maximum penetration of 7 feet. As indicated in figure 1, the roots show no difference in branching habit either above, in, or below the hardpan layer.

*Psoralea tenuiflora,* a widely distributed species and one of the most important legumes of the Great Plains, was also excavated at the same time. This species is characterized by a taproot and numerous large, widely spreading laterals, especially in the deeper soil. Frequently the taproot penetrates to 1 or 2 feet before branching, thus very little, if any, absorption occurs in the surface soil. Maximum depths of penetration of 8 to over 12 feet have been determined. The root habit is rather constant whether the plant grows in dry or moist situations. The specimen excavated at Yuma is shown in figure 2, where it may be seen that the bulk of the root system lies below the

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hardpan level. The tap was traced to a depth of 9 feet, at which point it was still 4 mm. in diameter and running rather vertically downward.

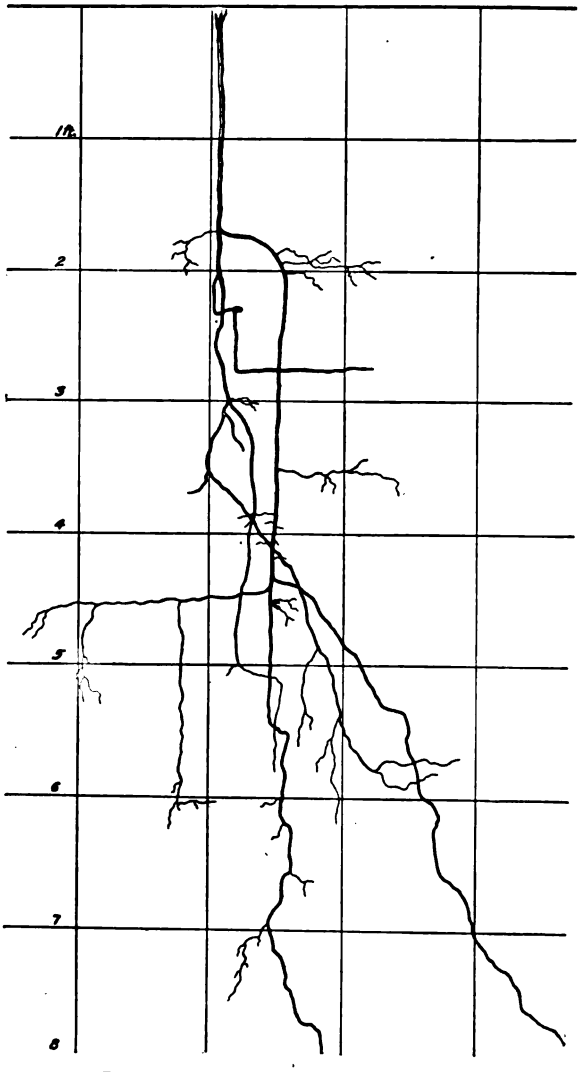


FIG. 2. Root system of psoralea, *Psoralea tenuiflora*.

Eight miles south of Limon, Colorado, in an area where the compact fine-sandy loam was underlaid at a depth of 2.5 feet with a hardpan, the roots of *Bulbilis, Psoralea,* the milk pink *Lygodesmia juncea,* and certain other native species were found extending far below the hardpan, some to a depth of over 7 feet.

Numerous studies on root development have been made in the vicinity of

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Burlington, Colorado. In an area 7 miles northeast of this town trenches were dug in the closed mat of buffalo grass and grama sod. The soil was similar to that already described (pp. 237–238) and was underlaid by hardpan at a depth varying from 1.9 to 2.3 feet. In thickness the hardpan varied from 0.5 to 1.6 feet. The soil was fairly moist to 3.5 feet, below which, though very mellow, it was powdery dry. Here the roots of buffalo grass were

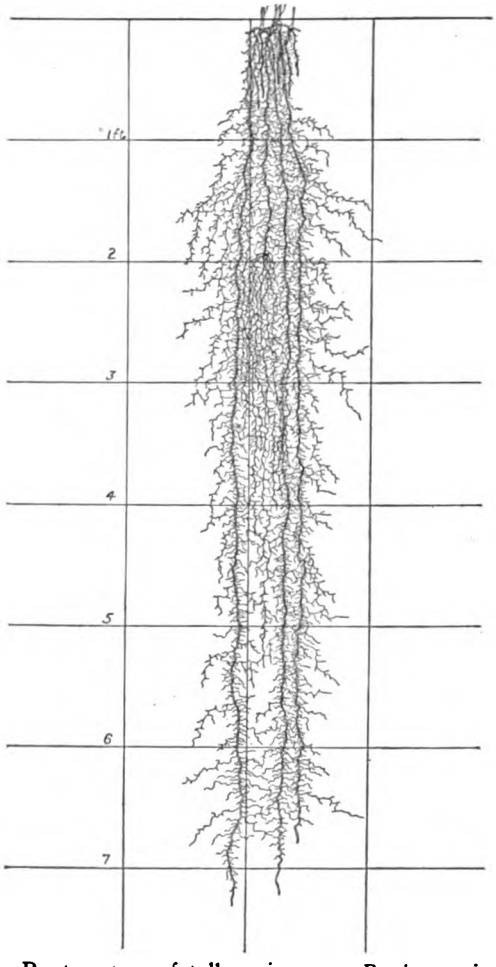


FIG. 3. Root system of tall panic grass, *Panicum virgatum*.

found in abundance at 4.3 feet, and some reached depths of 6 feet. The wire-grass clumps were rather small and no roots reached depths greater than 2.8 feet. Those of *Lygodesmia* were found to penetrate as deeply as those of *Bulbilis*.

Further studies in Burlington showed a similar distribution of the roots

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of the native vegetation. Blocks of sod about a foot square and 8 inches thick obtained from the prairie at Lincoln, Nebraska, were planted in the short-grass sod during 1920 and 1921 (Clements and Weaver, 1920). Among these were tall panic grass, *Panicum virgatum*, and bluestem, *Andropogon furcatus*. By July of the second season the former, aided by a fairly moist soil due to the collection of some run-off water, had reached a depth of over 7 feet—about its usual penetration—and was much more profoundly branched than normally (fig. 3). The roots of the bluestem, at least during the first season, were limited in growth by the depth of the moist soil, which did not extend beyond the hardpan (Table 3).

## The Root Distribution of Crop Plants

Crop plants, including both winter and spring wheat, rye, barley, oats, alfalfa, and sweet clover, have been repeatedly excavated and examined, not only at many stations in the Great Plains, but in the prairie region eastward. This affords an excellent basis for comparison and shows the effect of limited water-content upon root development. To avoid undue length these data are presented in tabular form, with the preliminary statement that root extent was in every instance in close agreement with depths of available water-content. In a few cases where the soil was moist to considerable depths, the roots responded by extending their area until they had reached rather normal development, as expressed in the more humid regions of eastern Nebraska. The working depth and maximum penetration of the roots under these more favorable conditions are appended in Table 4 for purposes of comparison.

A survey of Table 4 reveals at once an unusual root penetration of all of the cereals at the station 7 miles northeast of Burlington. These plants were excavated on a rather level area on June 29, 1919, at which time studies were also made in two different areas in the adjoining grassland. Here, at depths of 1.9 to 2.3 feet, the lighter-colored but not very firm-textured hardpan was encountered. It was 0.5 to 1.6 feet thick. The soil was fairly moist to 3.5 feet, below which it was powdery. However, in the fields of wheat, oats, and barley the soil was moist to more than 7 feet in depth, being easily molded into firm lumps with only slight pressure of the hand. An examination of the rainfall records shows that an excess of nearly 3 inches over the normal precipitation had occurred the preceding December and 4.3 inches in June. Moreover, the actual precipitation, owing to its very local nature on the Great Plains, may have been more here than where recorded at Burlington. Run-off from the grassland sod was probably much greater than from the cultivated areas, also snow may have added to the actual precipitation by forming drifts near the fences in the fields not far from the places of root excavation. Here, as in a field at Colby, Kansas, where seepage water from an irrigation reservoir had thoroughly moistened the hardpan, this layer, so conspicuous when dry, had been modified to such an extent that one could not distinguish it by casual examination from the soil above or below.

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TABLE 4. *Depth and thickness of hardpan and distribution of the roots of crop plants*
*All data are given in feet*

| Crop | Station | Depth of hardpan | Thickness of hardpan | Working depth of roots | Maximum depth of roots | Eastern Nebraska | |
|---|---|---|---|---|---|---|---|
| | | | | | | Working depth | Maximum depth |
| Winter rye | Yuma, Colo. | 3.6 | 0.8 | 2.2 | 2.8 | | |
| | Flagler, Colo. | 2.5 | 0.7–0.9 | 2.3 | 2.8 | | |
| | Burlington, Colo.[1] | 2.1[2] | 0.5–1.6 | 4.3 | 6.0 | 4.0 | 5.3 |
| | Limon, Colo. | 2.5 | 0.8 | 2.0 | 2.0 | | |
| | Colby, Kans. | 2.3 | 2.1 | 3.0 | 3.6 | | |
| Winter wheat (Turkey red) | Yuma, Colo. | 3.6 | 0.9 | 2.1 | 2.3 | | |
| | Sterling, Colo. | 2.8 | 0.8 | 2.7 | 2.8 | | |
| | Flagler, Colo. | 1.3 | 0.8 | 1.4 | 1.5 | | |
| | Burlington, Colo.[1] | 2.1[2] | 0.5–1.6 | 3.8 | 5.4 | 3.8 | 5.4 |
| | Colby, Kans. | 2.1 | 0.9 | 2.0 | 2.3 | | |
| | Limon, Colo. | 2.5 | 0.8 | 2.0 | 2.8 | | |
| Spring wheat (mostly Marquis) | Flagler, Colo. | 2.3 | 0.7–0.9 | 2.5 | 2.8 | | |
| | Limon, Colo. | 2.5 | 0.8 | 2.0 | 2.0 | | |
| | Burlington, Colo.[3] | 2.7 | 1.3 | 2.7 | 2.7 | 3.0 | 4.5 |
| | Burlington, Colo.[4] | 2.6 | 1.2 | 2.2 | 2.5 | | |
| Oats (mostly white Kherson) | Flagler, Colo. | 1.6 | 0.9 | 1.7 | 1.9 | | |
| | Colby, Kans. | 1.9 | 0.7 | 2.5 | 3.0 | | |
| | Burlington, Colo.[1] | 2.1[2] | 0.5–1.6 | 4.0 | 5.3 | | |
| | Burlington, Colo.[3] | 2.7 | 1.3 | 2.7 | 2.7 | 3.4 | 4.4 |
| | Burlington, Colo.[4] | 2.6 | 1.2 | 2.2 | 2.5 | | |
| Barley (Manchuria) | Burlington, Colo.[1] | 2.1[2] | 0.5–1.6 | 4.2 | 5.7 | | |
| | Burlington, Colo.[3] | 2.9 | 1.2 | 2.5 | 2.9 | 3.1 | 5.0 |
| | Burlington, Colo.[4] | 2.6 | 1.2 | 2.0 | 2.5 | | |
| Biennial white sweet clover[5] | Burlington, Colo. | 2.7 | 1.3 | 2.8 | 2.8 | 5 | 6.5 |
| Alfalfa[6] | Burlington, Colo. | 2.2 | 1.8 | 2.0 | 2.3 | 8 | 8–10 |

[1] Data from fields about 7 miles northeast of Burlington.
[2] No hardpan evident, depth judged from that in adjoining grassland.
[3] Station in Burlington, 1920.
[4] Station in Burlington, 1921.
[5] Examined in August of first season's growth.
[6] Examined in July of second season's growth.

Omitting this unusual condition, an examination of the table shows that in only 6 fields did the working depth of the roots of either the cereals or legumes extend below the upper surface of the hardpan. Three of these were near Flagler, two at Colby, and one in the field of sweet clover at Burlington. Data from these root studies, which extended over a period of 3 years, and years which were unusually favorable for crop growth, indicate conclusively

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that the supply of available water, which is the controlling factor to root extent in this region, occurs normally above the hardpan level. While a few of the more deeply penetrating roots extended from 0.1 to 0.6 foot into the hardpan layer, it more frequently happened that maximum root depth was

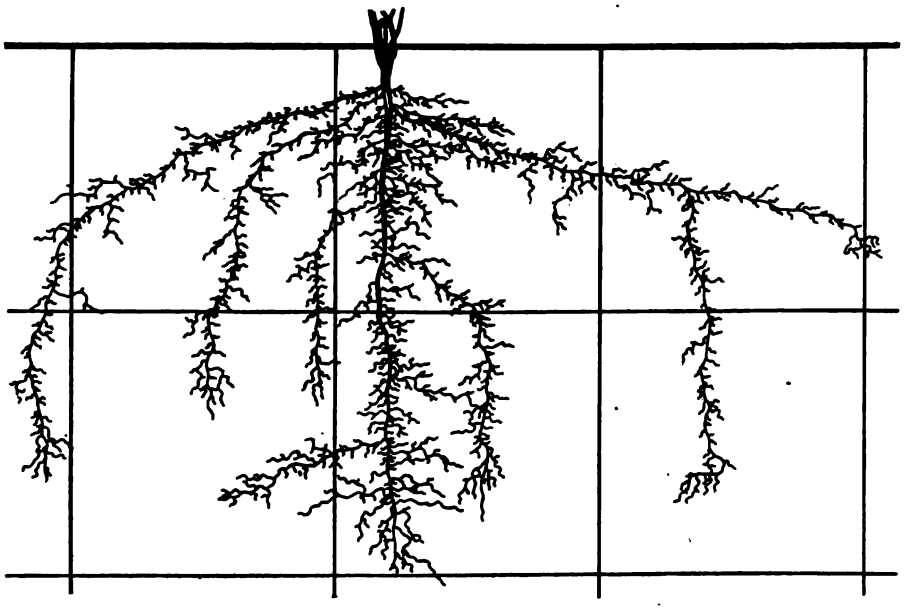

FIG. 4. Root system of Alfalfa during second year of growth.

either less or coincided with the depth of the latter. In only one case (rye at Colby) did the roots penetrate throughout the hardpan. Even the normally deep alfalfa was confined to approximately the surface 2 feet of soil, and its usually strong, poorly branched taproot underwent such profound modifications as scarcely to be recognizable (fig. 4).

The length of time during which the field had been broken from the native grassland had little effect upon root depth. This varied from one or two years (rye at Yuma) to over 20 years (rye at Flagler). Moreover, the effect exerted upon the root habit by the amount and placement of the available soil water much more than overbalanced any varietal differences in root habit as determined under more favorable conditions for growth (*cf.* fig. 5).

The habit of the roots of many of the native species of penetrating into the hardpan and often several feet below it, while growth of underground parts of crop plants is usually delimited by it, should be considered. The most logical explanation is that the relatively short-lived crop plants meet only occasionally (as exemplified at Burlington) with efficient precipitation of such amount that the hardpan (which in itself is no barrier to root penetration) is sufficiently moist to induce root growth. On the other hand, the long-

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lived native species (buffalo grass, psoralea, etc.) at some time during their life must experience periods when not only the hardpan, but also the soil below, is sufficiently moist to induce root growth. How long these roots, once

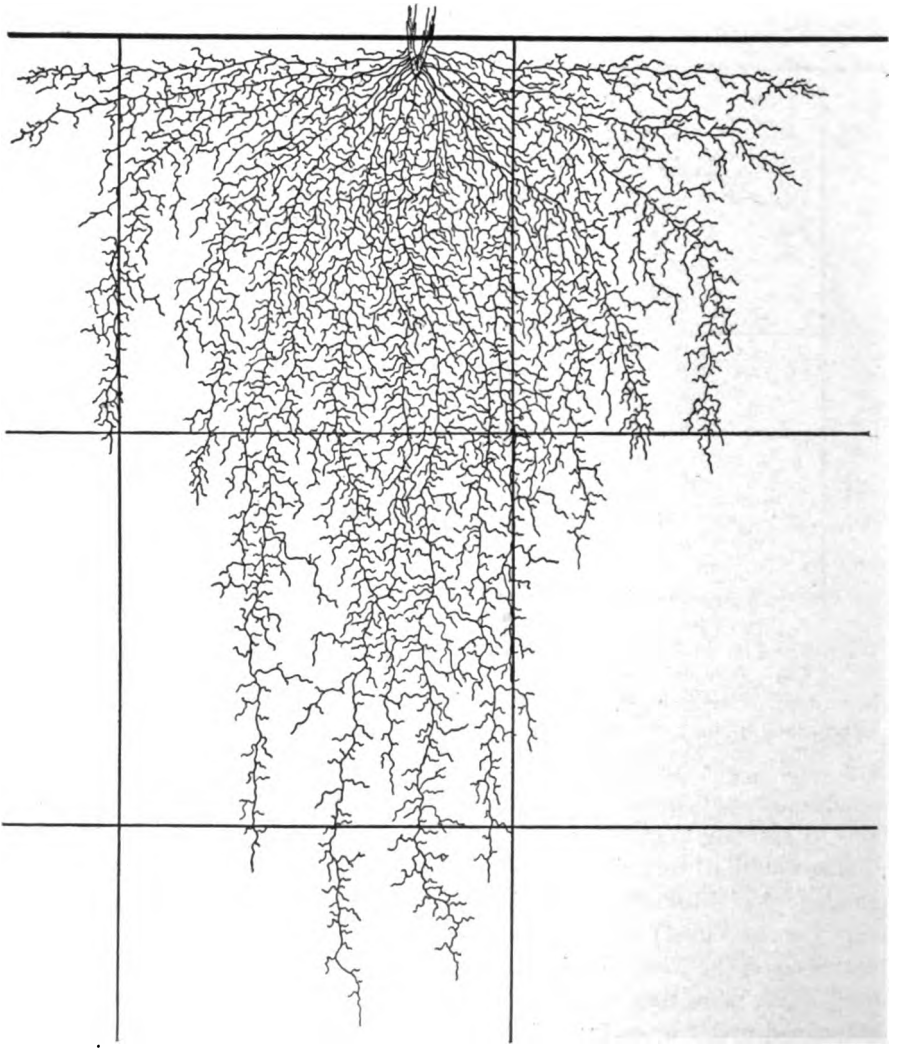

FIG. 5.- Root system of mature White Kherson oats.

formed, remain alive and active is yet to be determined. The ability of these native species to grow in soil too dry for good development of ordinary mesophytic crop plants may also play a part.

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## Summary

A so-called hardpan exists in the soils over much of the Great Plains region at depths of 1.4 to 3 feet. It varies in thickness from 8 inches to over 1.5 feet. In some localities it appears to be due largely or entirely to the calcareous nature of the soil. In others it is clearly caused by the concentration and cementing effect of colloidal clay aided in part by the carbonates. Water-content determinations show that the hardpan occurs at approximately the normal depth of water penetration. When moist it disappears, but reappears again upon the desiccation of the soil.

Available water is the controlling factor of root extent in this region and occurs normally only above the hardpan. Thus the hardpan in general delimits the depth of penetration of crop plants, but under exceptional moisture conditions they may extend their roots 5 or 6 feet deep. Many of the native species penetrate into the hardpan regularly, not only extending their roots through it, but often several feet beyond. No modifications in root habit were apparent in the hardpan layer. Since roots will not grow far into dry soil, the logical explanation of the fact is that at some time during the life of these perennials water must penetrate through the hardpan. How long these deeper roots remain alive after the subsoil is again desiccated is undetermined.

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# THE RELATION OF THE NYMPHS OF A DRAGON FLY (*Libellula pulchella* DRURY) TO ACID AND TEMPERATURE[1]

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## Materials and Methods

The dragon-fly nymphs were collected in a quiet muddy pocket of a badly polluted small stream called the "Boneyard," which flows through Champaign-Urbana, Illinois. All the nymphs were found buried in mud at a depth of one and a half feet from the surface of the water. Collections were made on two different occasions—in the fall on October 3 and in the spring on April 24. On both occasions this quiet muddy pocket contained a considerable number of the nymphs about fully developed. The mud in which they were living on April 24 was acid, pH 6.4, and the surface of the water only slightly less so, pH 6.6. This is a higher degree of acidity than is usually the case. Most streams are appreciably alkaline. No stream has been recorded, so far as I know, that normally showed a hydrogen-ion concentration greater than 5.8. Very few nymphs were found anywhere else in the stream, and then only in mud under debris such as pieces of wood and tin cans.

In my experiments I used a box of thin sheet iron, about two feet long, one and a half inches wide, and one and a half inches deep. A vertical row of holes was punched in the middle of the box on each side to let out the water. An acid solution was produced by mixing water and acid in a Mason jar in such proportions that the desired pH values could be obtained. The water used throughout was aerated University of Illinois water; the acid was hydrochloric. Except in experiments where special temperatures were used, the range was from 18°–24° C., generally around 20° C. In order to insure uniformity of light, two 50-watt Mazda lamps were placed immediately above and at equal distances from the ends of the box. The pH determinations were made by the colorimetric method, using standard buffer solutions at the lower concentrations, and McClendon's color chart for concentrations greater than pH 4.0. The nymphs, until used in the experiments, were kept in shallow jars containing gravelly mud and rotting leaves, with some two inches of water. The jars were immersed in cool running water of an average temperature of 20° C. Since the nymphs are cannibalistic, they were not fed. From time to time as their water became foul they were given a clean supply.

[1] Contribution from the Zoological Laboratories, University of Illinois, No. 203.



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## Experimental Results

### Reactions

*Acid gradients.*—To produce an acid gradient, the acid solution from the Mason jar was allowed to flow in at one end of the box, and unmodified water was allowed to flow in at the other end at the same rate. The two liquids mixed sufficiently to produce a definite gradient, and flowed out through the row of holes in the middle of the box. At first a slight acidity was used, ranging from pH 6.4 to 8.4. The results are given in Table I.

TABLE I. *Response of dragon-fly nymphs to slight acidity and alkalinity*

Readings every two minutes (after the first five minutes). Every 5th reading

| Shown | Acid | | | Neutral | | Alkaline | | |
|---|---|---|---|---|---|---|---|---|
| pH | 6.4 | 6.4 | 6.6 | 7.1 | | 8.2 | 8.4 | 8.4 |
| 1st | 4 | 2 | 2 | 0 | 4 | 2 | 1 | 5 |
| 5th | 5 | 0 | 2 | 2 | 2 | 2 | 2 | 5 |
| 10th | 4 | 2 | 0 | 2 | 0 | 2 | 3 | 6 |
| 15th | 2 | 2 | 2 | 0 | 4 | 2 | 0 | 8 |
| 20th | 1 | 5 | 2 | 1 | 3 | 0 | 2 | 6 |
| 25th | 3 | 1 | 1 | 0 | 2 | 3 | 1 | 9 |
| Total all readings | 82<br>16% | 47<br>9% | 34<br>7% | 36<br>7% | 57<br>11% | 39<br>8% | 36<br>7% | 167<br>33% |

Rate of flow—55 c.c. per minute.
Temperature—Acid end, 21°.5 C.; alkaline end, 22°.5 C.
Stock, in laboratory three months. Number of individuals, twenty.

*Note.* The 8 columns in this and the following tables represent 8 sections of the experimental box, and the numbers in the columns represent the number of nymphs in each section at each reading.

It will be seen that some preference was shown for the alkaline end, about twice as many nymphs congregating in this end as in the other. But it will also be noticed that considerably more nymphs collected at the acid end than anywhere else except the alkaline end. This "bunching" at either end was characteristic throughout the acid-gradient experiments. Subsequently stronger acidities were used.

Table II illustrates the reaction that was typical of a number of experiments in each of which the range of pH values was largely the same. The "bunching" of the nymphs was, however, not nearly so marked in this particular experiment as was generally the case. In this and subsequent tables the rate of flow was 26 c.c. per minute.

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TABLE II. *Response to acidity and alkalinity*

Readings every three minutes (after the first five minutes)

| pH 5.0 | – | 5.8 | 7.3 | | 8.4 | – | 8.6 |
|---|---|---|---|---|---|---|---|
| 2..... | 0 | 4 | 5 | 2 | 2 | 3 | 2 |
| 2..... | 1 | 3 | 5 | 3 | 3 | 1 | 2 |
| 4..... | 1 | 1 | 6 | 2 | 1 | 2 | 3 |
| 4..... | 1 | 1 | 6 | 2 | 1 | 1 | 4 |
| 4..... | 1 | 2 | 3 | 3 | 1 | 2 | 4 |
| 4..... | 2 | 2 | 2 | 0 | 4 | 1 | 3 |
| 5..... | 1 | 2 | 3 | 0 | 4 | 2 | 3 |
| 3..... | 2 | 2 | 5 | 0 | 3 | 2 | 3 |
| 28..... | 9 | 17 | 34 | 12 | 19 | 14 | 25 |
| 18%.... | 6% | 11% | 21% | 7% | 12% | 9% | 16% |

Temperature—Both ends, 18°.0 C.
Stock, in laboratory three months. Number of individuals, twenty.

An example of the effect of a marked acidity is shown in Table III. It will be observed that a very decided "bunching" took place at either end.

TABLE III. *Response to strong acidity and slight alkalinity*

| pH | 2.5 | – | 5.5 | – | 6.2 | – | – | 7.8 | |
|---|---|---|---|---|---|---|---|---|---|
| | 7 | 0 | 0 | 1 | 1 | 0 | 1 | 10 | after one hour. |
| | 7 | 0 | 0 | 1 | 2 | 0 | 0 | 10 | after three hours. |

Temperature—Both ends, 22°.5 C.
Stock, in laboratory ten days. Number of individuals, twenty.

At the conclusion of this experiment the seven individuals in the acid end were placed in a separate jar. After a week only one was dead. After eighteen days four had been attacked by fungi and were dead, but the remaining two were alive and vigorous. The individuals not in the acid end did not show any fungus infection. The results shown in Table III were corroborated a number of times in experiments in which the range of acidities employed were practically the same.

Table IV represents an experiment in which a pH of 1.0 was reached one fourth down the box. At the time I had no way of determining stronger acidities, so the concentration in the acid end of the box remained unknown, though it must have been considerably greater than pH 1.0. The nine individuals in this end were placed in a jar to themselves, and after a week all but one were living and apparently vigorous.

TABLE IV. *Response to very strong and moderate acidity*

| pH | – | – | 1.0 | 2.0 | 6.0 | – | – | | |
|---|---|---|---|---|---|---|---|---|---|
| | 8 | 0 | 0 | 1 | 2 | 1 | 2 | 2 | after one and a half hours. |
| | 7 | 0 | 0 | 2 | 0 | 1 | 3 | 2 | after two hours and ten minutes. |

Temperature—Both ends, 24°.0 C.
Stock, in laboratory four weeks. Number of individuals, sixteen.

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*Uniform acidity.*—The acid solution only was allowed to flow into the box, at the usual rate of 26 c.c. per minute, and had to be continuous to produce a constant pH value. Out of eight individuals, from stock in the laboratory four weeks, in a uniform acidity of pH 1.0, two were at one end and six at the other. This shows that the nymphs can stand a constant pH of 1.0 at a temperature of 21° C. for twelve and a half hours. At the end of this time they were all alive and apparently vigorous.

### Uniform Acidity with High Temperature

In an experiment in which the pH was uniformly 1.0 and the temperature was 34°.5 C., six nymphs showed distinct irritability immediately on being placed in the experimental box. They showed no inclination to bunch at any time. At the end of an hour one was dead. Two hours later there was no further change. Eleven hours later the acid tube was found clogged and the pH was about 7.0, but the temperature was the same, 34°.5 C. All the individuals were alive. Considerable of the acid had been used, enough for four or five hours at a pH 1.0 flow. The pH was adjusted back to 1.0, and after four hours, or eighteen hours from the beginning of the experiment, three of the nymphs were still alive, and were living three days later. With a pH of 1.0 and the temperature raised to 40°.5 C., twelve individuals showed, as in previous experiments, the same distinct irritability with no tendency to bunch, and were all dead in forty-five minutes.

### Increased Temperatures Alone

No acid solution was used in this experiment, and the water, that of the University, was alkaline, pH 8.0. Five out of six nymphs appeared unharmed at a temperature of 37°.5–38°.0 C. for eighteen hours. Five fresh individuals were placed in the box with a temperature of 40°.0–41°.5 C. Two nymphs were dead after eight hours. Thirteen and a half hours later another was dead, and the two remaining were nearly dead. At a temperature of 42°.5 C. six fresh individuals were all alive after one hour, but all dead after four hours and ten minutes. At 44°.0 C., of four individuals, one was dead in eleven minutes, another in 25 minutes, and the remaining two in one hour and five minutes. At 45°.0–46°.0 C. the nymphs will live as long as nineteen minutes. At 50°.5 C. they will live only a few seconds.

## Conclusions

The outstanding result of these experiments is the great hardiness of the nymphs of *Libellula pulchella.* They lived very well for more than six months in alternating foul and fresh water. They lived apparently unharmed in water as strongly acid as pH 1.0, with more or less indifference to the degree of acidity present. The literature I know of that deals in pH values seems to agree that the animals experimented on succumb to a pH of 5.0, and

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select an environment with a reaction around neutrality. Of nine species of fish, the selection ranged from pH 6.8 to 8.0. Furthermore, the nymphs of *Libellula pulchella* are apparently uninjured by a temperature distinctly greater than that of mammalian blood.

The foregoing experiments were carried on under the supervision of Prof. V. E. Shelford. Sincere thanks are extended to him for many helpful suggestions offered during the progress of the work.

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# ECOLOGICAL NOTE ON THE BIRDS OBSERVED AT THE BIOLOGICAL STATION OF THE UNIVERSITY OF MANITOBA

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It is seldom that one has the opportunity of studying a number of well-defined habitats of birds in a small circle of two miles diameter, and of determining how far these habitats overlap and to what extent they are correlated and interchangeable. This opportunity arose so admirably in June and July of 1920 at the new Biological Station of the Manitoba University at Indian Bay, Shoal Lake, Lake of the Woods, Manitoba, that I am tempted herewith to outline the main characteristics that future students may investigate them further.

The Biological Station is situated at Waugh (Indian Bay), the terminus of the Greater Winnipeg Water District Railway. For the last two years Winnipeg has received its entire water supply from Shoal Lake. Since the present railway service leaves much to be desired, and is but little patronized by holiday makers, Indian Bay still enjoys its pristine wildness. Despite the efforts of the Indian School on Snowshoe Bay, the Indians are much the same as they have always been. There is a small permanent population of white men in connection with the water works and railway, but they are busy men and have disturbed the wild life of the place but little. This year the Biological Station has therefore offered a unique chance of studying the natural bird life of the district. Only a single artificial factor had to be considered—the large gravel pit which supplied the materials for the dyke built across Falcon Bay. Future students will be able to note the changes that are bound to occur in the avifauna of the place as the railway service improves, and brings with it the inevitable campers, and perhaps even enterprising agriculturists.

The buildings of the Biological Station are situated on the edge of Indian Bay. Within a mile can be studied at least seven well-defined faunal habitats. These are:

1. The lake itself.
2. The forest surrounding the lake.
3. The muskeg lying beyond the belt of forest.
4. Several small marshes.
5. The gravel pit.
6. The islands of the lake.
7. The scrub.



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These were studied from the point of view of feeding and nesting zones. Out of the seven enumerated, only two were entirely self-supporting—*i.e.*, only two contained nesters that found all they required within their nesting area—and were not forced to wander into other zones.

The lake was one. True, it was used as a feeding area by numerous species, and as a nesting zone by comparatively few, but such as they were, the latter found the lake all-sufficient for their needs. They included only a few ducks and an odd pair or two of loons. Grebes of any sort appeared to be absent. Black terns were abundant, but their breeding quarters were located on Snake Lake more than a mile from Indian Bay. Why they came so far and in such numbers to feed was not definitely ascertained. Their own lake was apparently as well suited, but it was more or less choked with wild rice, and this may have been a determining factor. As soon as the young could fly they were escorted to Shoal Lake and stayed there.

The forest on the edge of the lake was the most important of the seven habitats, in that it held a greater number of nesting species than any other. Of these the small birds found in it all that they required. Insect life was abundant and berries were plentiful. A number of sparrows and warblers were characteristic of the forest, but particularly the white-throated sparrow, white-and-black warbler, and redstart. The red-eyed vireo, crow, and ruby-throated humming bird were perhaps equally ubiquitous. The ruffed grouse, robin, hermit and veery thrushes, oven bird, chickadee, and purple finch, if less plentiful, were very characteristic. The various woodpeckers belonged to this zone, but they recognized subdivisions not known to the other species. The downy was perhaps the only one that was general throughout, patronizing wet and dry areas alike. It extended right into the dead-tree areas of the muskeg itself. The hairy, flicker, and sapsucker—the last in the greatest numbers—were fairly general, the three-toed arctic and pileated being by far the scarcest and very local. Both seemed to be confined to the large tree areas. But all of these nested and lived entirely within their own zone. It was amongst the larger species that the majority of nesters occurred that had to travel afield for their food supply. Most notable were the osprey, turkey buzzard, and great blue heron. The ospreys, living entirely on fish, had to hunt over the lake. On windy days they would travel systematically round the borders of the bay, searching for quiet spots in which they could see their prey. The herons often traveled far afield to satisfy their needs, sometimes even visiting the small marsh referred to below, two miles from their home. The turkey buzzards regularly carried out huge peregrinations in search of food, mostly on the edge of the bay.

Another breeder of the forest, whose nesting sites were confined to the small lichen-covered patches of rock, the nighthawk, appeared also to get his main supplies far afield, though when the young had hatched these excursions were much curtailed. This rather suggests that these flights savored as much

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of pleasure as they did of necessity. This assumption is borne out by the fact that scores of these birds, during the incubating period, would sit for lengthy stretches of time in the mornings and the evenings between the metals on the railway track, but did not deposit eggs there. This habit appeared to play part in a social function of sorts, but it also ceased when the eggs were hatching.

The great horned owl, represented by but a single pair, was located on the edge of the muskeg and they may indeed have done some of their hunting over it, but their loud hootings were heard always in a small circle round their presumed home. They were in all probability true denizens of the forest.

The muskeg, by far the most extensive of the seven habitats, stretching as it did forty miles or more to the west and north, was, ornithologically speaking, extremely poor. Four species only were found to be constant to it—the short-billed marsh wren, swamp sparrow, kingbird, and Maryland yellow-throat. Mostly of the type known as floating muskeg, it resembled a huge meadow, all of which was well stocked with the two first of these species. Here and there on the more stable parts were clumps of bushes. These provided nesting places for the last two. All four were found to be stay-at-home birds, but only the wren was found here and nowhere else. A few yellow-throats and kingbirds were seen elsewhere, although the percentage of those outside the muskeg was small. Ducks may have nested here also, but we got no evidence to that effect. Two trips were made through extensive stretches of this habitat, one at the end of June, the other at the close of July. On the first no ducks at all were seen, while on the latter they were plentiful with well-grown young. These may have, and probably did, swim down the river from the little lakes connected with the muskeg.

An interesting feature of the muskeg was the frequent outcroppings of rock forming small heavily timbered islands. Owing to lack of equipment in this the first year of the Biological Station, in the matter of boats and canoes, the muskeg was rather neglected, and the fauna of these islands was never investigated. That they harbored numerous hawks, such as the broad-winged and probably the red-shouldered, is certain. These were not found nesting in the forest proper.

Here and there within the area occurred small marshes. These differed from the muskeg in consisting of patches of open water with rushes and flags as the characteristic plants. A canoe was portaged to one of these lying to the north of the railway track and about a mile from the Biological Station, and a number of days were devoted to the study of its avifauna. Its nesting inhabitants included the following: mallard, bittern, coot, Carolina and Virginia rails, long-billed marsh wren, red-winged blackbird, and swamp sparrow. With the exception of the blackbirds and to some extent the bittern, all these birds bred and fed within their own zone. The bittern used to make regular trips to the adjoining Falcon Bay, where the crayfish, one of his staple foods,

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was abundant. These flights were taken with monotonous regularity at certain hours of the morning and evening. A large percentage of his food was, however, obtained in the marsh itself. The redwings regularly hunted in the brush on the edge of the lake, scores even crossing to some of the islands two miles or more from their breeding station.

Many long hours were spent in this mosquito-ridden marsh, hidden in the bottom of a reed-covered canoe, to obtain notes on the habits of its birds. It was intended to spend at least one night here, but without mosquito netting, an impossibility when binoculars and a gun have to be used, no man could have stood it and remained sane. As an alternative several afternoons and evenings till nightfall were spent on the spot, the watch being resumed again at 2.30 in the morning. One thing is certain as the result of these investigations—the supposedly nocturnal rails are anything but nocturnal, at this time of year at all events. At about sundown every rail disappeared. The coots, too, became quiet, and the crying of the nighthawk overhead and the booming of the bittern from the heart of the reeds were the only sounds that broke the evening stillness. In the mornings as the marsh was approached, with the first gray streak of dawn just showing in the east, never a sound came from it. Twice a list was made of bird notes in the order in which they were heard. Since both lists coincide very well, it may be worth while quoting: song sparrow, swamp sparrow, red-eyed vireo, redwing, kingfisher, rails, goldfinch, coot, long-billed marsh wren, olive-sided flycatcher, kingbird, short-billed marsh wren, swift, rough-winged swallow, mallard, yellow warbler. Nighthawks were about from the time of arrival and remained in view till an hour after sunrise. In contrast to their evening flights, these birds were, as a rule, entirely silent in the mornings. Of the whole list many were, of course, not nesters in the marsh, but all nested within a short distance of it. The short-billed marsh wren did not nest here, but in the muskeg across the railway track, while the long-billed species was never found nesting in the muskeg, but always in true marsh. The swamp sparrow was common to both.

The song sparrow was invariably the first bird heard and began to sing as soon as the first signs of day appeared. No sight or sound of the rails was ever apparent until sunrise, and it was not till an hour later that they appeared in any numbers. Thence onwards for about two hours they were at their liveliest, all coming out to feed on the open edges. During the middle of the day they retreated, becoming noisy again about two hours before sunset. But with the fall of night they and the coots with them retired like all other birds. Soon after sunrise the bitterns also came forth to feed. It was a rare treat to watch these ungainly birds, in the company of coots and two species of rail, besporting themselves within a few yards of the hidden canoe. The long-billed marsh wren was very secretive the whole time. Very few good views of it were obtained. Even its singing was done in the heart of the reeds

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instead of from the top of some tall vantage point as in the case of its short-billed relative of the muskeg.

Except for the birds that bred in the marsh, it was little used as a feeding ground. The olive-sided flycatcher, which had its nest presumably in a clump of dead trees adjoining, much patronized by the tree swallow, hawked it regularly, as did the swallows also. Rough-winged swallows were occasional visitors. Once in a while the great blue heron put in an appearance.

Another small habitat of exceptional interest was found in the gravel pit. This is about a quarter of a mile in length and some hundred yards across, with banks between twenty and thirty feet high. Its bottom was at first marshy, but, owing to the dry summer, it subsequently became solid. Artificial and man-made, it illustrated well the ever-interesting fact, both botanically and faunistically, that all living things are ready and waiting to colonize any new suitable ground that may offer. The pit is only a few years old, yet it already has a rich flora. In this district open areas (excepting those of muskeg and rock) and sand banks are entirely wanting. Hence one would not expect birds requiring these conditions to occur here. The gravel pit has, however, provided both for the last year or two. As a result it has attracted to itself an avifauna quite peculiar, if somewhat meager. But its very small area must be taken into account; for its size it has done remarkably well. Had time permitted it would have been of the utmost interest to investigate the insect life of the zone. No doubt some peculiar species would have been found. Of birds it could boast three kinds entirely to itself. It held the only pair of vesper sparrows in the district. These lovers of open spaces had their nest at the foot of one of the banks. The east bank housed a flourishing little colony of rough-winged swallows, the only ones of their kind. The only spotted sandpiper collected within many miles of the station was secured here. It was one of a pair and proved to be the female, ready to lay. This was late in the season and the birds had evidently been disturbed elsewhere and were seeking new quarters. Had they been left alone, they would no doubt have bred in the pit, the only suitable site in the locality.

Though the kingfisher has probably nested at Indian Bay from time immemorial, there is just as little doubt that it has never bred in such numbers as of recent years, for the simple reason that the rocky edges of the lake did not offer enough nesting sites. The gravel pit, with its soft, sandy sides, was, however, conveniently dug, and it now holds what might almost be termed a colony of kingfishers. More than a dozen nesting holes were in use here this year, and the bird is now one of the most prominent at the station. In this connection it is interesting to note that here and there in the forest other small sandpits have been dug. These were experimental in nature and left as dug, many of them only a few feet across, with banks about eighteen inches high. All of these, some more than a mile from the lake, held each its pair of breeding kingfishers, a further example of colonizing ability.

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The gravel pit was much used as a feeding ground by birds from other zones, particularly before it dried up. With the bronzed grackles it was a particularly favored hunting area; goldfinches and siskins patronized it regularly; bitterns came from time to time; the ubiquitous song sparrow fed here, but apparently did not breed. This was one of the few spots on which the house sparrow was regularly to be seen. It bred in very limited numbers on the railway buildings adjoining.

Two zones remain to be mentioned, neither of which was worked out fully. By scrub I mean those areas on which the trees have been felled and have not yet been replaced by full growths, and the natural scrub fringing the marshes and the muskeg. The latter was not extensive, nor was it as well defined as the others. It should probably be further subdivided. Characteristic birds were the catbird, Maryland yellow-throat, goldfinch, rose-breasted grosbeak, chestnut-sided warbler, song sparrow, yellow warbler, black-billed cuckoo, chipping sparrow, cedar waxwing, and marsh hawk. The first three showed a distinct preference for the brush on the water's edge. Of the others, some favored brush interspersed with trees, but none was found in the forest proper.

As a habitat the islands need a great deal more scrutiny. All were well stocked with birds, the redstart, song sparrow, and crow being perhaps the most widely distributed. A few species were noted on the islands that were never observed on the mainland. They include the palm warbler, yellow-bellied flycatcher, and water thrush. The olive-backed thrush, comparatively scarce on the mainland, occurred on several of the islands.

A few birds showed no preference for any of the above zones and are difficult to place. They include the chimney swift, which nested in the chimney of one of the Biological Station buildings and in some numbers on the railway water tank; the phoebe, which seemed to nest anywhere and everywhere on buildings and fallen tree trunks; the bronzed grackle, of which there was one large colony in a patch of swampy scrub freely sprinkled with trees; the tree swallow, sharing the ground of the grackle and nesting also elsewhere, *e.g.*, telephone poles, mostly on open sites; and lastly the house wren, not plentiful, but nesting in the most unlikely and unclassifiable places.

The total number of species observed during the summer was almost 106.[1] Of these nearly 90 were in all probability breeders. In the above notes only those are included which were found in sufficient numbers to give one a definite idea as to the zones they preferred.

[1] "The Auk," Vol. 39, No. 2, April, 1922.

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# REVIEWS

## The Evolution of Long Island[1]

The author starts with the ecological viewpoint and endeavors to trace the influence of three principal environmental forces on the history of the island. These are the climate and soil of the island itself, the sea, and the influence of the hinterland or proximity to a large and spreading center of population. In the early history of the island, when the population depended chiefly upon agriculture and fishing, the first two forces were, practically speaking, alone effective. But gradually the influence of the hinterland made itself felt, until recently through improved transportation the population of New York City has extended out onto Long Island for homes, for recreation, and for garden products. Thus the first two forces, though still operative, are now overshadowed by the third.

To the ecologist the chapter on the pine-barrens will be almost the only one of special interest in this rather sketchy and popular account of the history of Long Island. There has been a good deal written on the history of the island in the past, some of which yields valuable information about the early condition of the country. From Thompson, Prime, Furman, Onderdonck, J. T. Adams, the Gardiners, and hosts of others a great amount of information about the early condition of the vegetation on Long Island has been gleaned, to which the present volume appears to add nothing aside from its viewpoint.

More than any of these earlier historians, however, the author of the present volume lays emphasis on the great pitch-pine forests in the center of the island. He shows that just after the Revolution they yielded enough wood to build up a very considerable business in firewood, which continued until the disastrous forest fires, which followed the introduction of the Long Island Railway in 1844, put a stop to these shipments. As a record of facts as to what has been done in the pine-barren area in the way of using them, this chapter is useful. But there is nowhere to be found in it a hint of the significance of those facts in the succession which is being followed out on different sites in the barrens. The author might well have copied the diary of our greatest colonial agriculturist who wrote of this area (22 April, 1790) that it "is too poor to admit inhabitants or cultivation, being a low scrubby oak, not more than two feet high, intermixed with small and ill-thriven pines." General Washington gives us in these few words a better picture of the facts

[1] Gabriel, R. H., "The Evolution of Long Island," pp. 1–194, map. Yale University Press, December 31, 1921.



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of succession near Coram than this latest addition to the already voluminous history of the island.

NORMAN TAYLOR

## A NEW CLASSIFICATION OF SOIL MOISTURE[1]

One of the most important and unfortunately also one of the most complex ecological problems is that of soil moisture. The time has passed in which data on soil moisture alone were considered of value. We need to know the water available to plants, not merely the total quantity. Pending the formulation of basic physical principles of soil moisture some method must be used for separating the available from the unavailable water. It is now pretty generally recognized that for any given soil the water unavailable to plant roots is a fixed quantity which to all intents and purposes is a constant depending on the physical properties of the soil. This quantity Briggs and Shantz[2] have called the wilting coefficient. The reviewer is not unaware that acceptance of the wilting coefficient is not complete, and that there is still a tendency to consider it correlated with atmospheric conditions as shown by Caldwell[3] and by Shive and Livingston.[4] Yet a mass of data, some published and some unpublished, show that plants wilt when the soil water has been reduced to a certain rather definite point, regardless of the rate of evaporation. It is true that high evaporation to which a plant is not adapted will cause it to wilt while there is still available water in the soil. If the change is sudden enough, a plant can be made to wilt in water culture. Shull's work on the water-withholding power of soils[5] shows that when the water has been reduced to a certain point the force necessary to extract small additional quantities increases very rapidly. The curve of increasing force with decreasing water is very sharp, as shown on page 25 of Shull's paper. Thomas, in a valuable paper on the "Aqueous vapor pressure of soils,"[6] gives curves showing an equally sharp drop in vapor pressure when the soil moisture decreased to a point which corresponded approximately with the wilting co-

[1] Bouyoucos, George, "A New Classification of the Soil Moisture." Soil Sci., Vol. 11, No. 1, pp. 33–47, 1921.

[2] Briggs, L. J., and Shantz, H. L., "The Wilting Coefficient for Different Plants and Its Indirect Determination." U. S. Dept. Agr., Bur. Plant Industry, Bull. 230, 1912.

[3] Caldwell, J. S., "The Relation of Environmental Conditions to the Phenomenon of Permanent Wilting of Plants." Physiological Researches, Vol. 1, No. 1, pp. 1–56, 1913.

[4] Shive, J. W., and Livingston, B. E., "The Relation of Atmospheric Evaporating Power to Soil Moisture Content at Permanent Wilting in Plants." Plant World, Vol. 17, pp. 81–121, 1914.

[5] Shull, Charles A., "Measurement of Surface Forces in Soils." Bot. Gaz., Vol. 62, No. 1, pp. 1–31, 1916. Reviewed in Journal of Forestry, Vol. 15, No. 1, pp. 110–117, 1917.

[6] Thomas, Moyer D., "Aqueous Vapor Pressure of Soils." Soil Science, Vol. 11, No. 6, pp. 409–434, 1921.

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efficient (pp. 421 and 422). It is evident, then, that considerable differences in pull exerted by the roots of different species of plants would not materially affect the percentage of water left at permanent wilting.

The water in the soil has generally been divided into gravitational, capillary, and hygroscopic. But Briggs and Shantz's work show that part of the so-called capillary water is available and part unavailable to plant roots. The water left at permanent wilting includes much more than the hygroscopic moisture, although Alway has shown that even some of the hygroscopic water may have a high value for the maintenance of life in certain desert legumes.[7]

Bouyoucos has developed a new classification based on the freezing point lowering of the different portions of soil moisture determined by the dilatometer method. This classification is as follows:

Gravitational
Free
Unfree { Capillary-adsorbed
Combined { water of solid solution or
water of hydration

The gravitational water needs no comment. The free water is that which freezes for the first time at a temperature of —1.5° C. The capillary-adsorbed water is that which freezes finally at the supercooling of —4° C. and lower. The combined water does not freeze at all even at —78° C.; this is the water of hydration in the soil colloids.

Determinations were made of the percentages of water which came under the above categories, except gravitational, in 73 soils. As was to be expected, the heavier soils contained the larger percentages of unfree water and smaller percentages of free water. The unfree water ran from 0 in quartz sand, and 4 percent in coarse sand, to 84 percent in Minnesota Superior Clay and in Cecil Clay from Jackson County, Louisiana. The percentages are constant for any given soil.

A direct comparison between the wilting coefficient and dilatometer results shows that the percentage of moisture which fails to freeze at —1.5° C. agrees very closely with that at which plants begin to wilt, "indicating that the wilting coefficient of soils is at the point where free moisture ends and the capillary-adsorbed moisture begins."

It is significant that Bouyoucos arrived, by an entirely different route, at practically the same position as Briggs and Shantz. The author states (p. 43) that in the light of the dilatometer results we see that plants wilt at the wilting coefficient, not because the rate of movement of soil moisture is too slow, but because it does not move at all. (See also Journal of Forestry review cited in footnote 5, p. 116.)

[7] Alway, F. J., "Studies on the Relation of the Non-available Water of the Soil to the Hygroscopic Coefficient." Univ. of Neb. Agr. Exp. Sta. Research Bull. 3, 1913.

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In spite of the correlation which he found between his dilatometer results and the wilting coefficient, the author states that determination of the wilting coefficient by means of the plant, besides being tedious and time-consuming, is not accurate nor constant. He accepts the misconception, based on the work of Caldwell and of Shive and Livingston, that "permanent wilting is a function of atmospheric evaporation," discussed in the first paragraph above. This, however, bears only on his argument that the dilatometer offers a better method of determining unavailable moisture than direct determinations by use of plants.

On the whole, the work is of much significance in the conception of soil moisture presented and in giving another method of measuring the unavailable water of soils.

BARRINGTON MOORE

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## ZOOLOGICAL ABSTRACTS[1]

**Crampton, Henry E.** On the differential effects of the influenza epidemic among native peoples of the Pacific Islands. *Science,* n. s., **55**: 90–92. 1922.

In the late influenza epidemic the natives of the Society Islands suffered a mortality of 15 to 25 percent; the half-caste population lost a distinctly smaller percentage; and the white inhabitants suffered little mortality. The incidence of the disease was about the same for all the three classes mentioned. On the island of Saipan in the Mariana or Ladrone group the Mariana Islanders suffered a mortality in excess of 12 percent, while among the Caroline Islanders, equal in total number, the mortality was less than 1 percent. These facts indicate distinct differences in natural resistance to the disease in the various races considered. L. R. Dice.

**Evermann, B. W., and H. W. Clark.** Lake Maxinkuckee, a physical and biological survey. *Indiana Dept. Conservation,* Publ. No. 7: 2 v., il. 1920. Rev. Ecology **2**: 311, '21.

Many data on the environmental conditions in and about Lake Maxinkuckee, Indiana, and valuable annotated lists of species of animals. Little attempt is made to correlate the environmental data with the distribution or life-histories of the animals. L. R. Dice.

**Hildebrand, Samuel F.** Top-minnows in relation to malarial control, with notes on their habits and distribution. *U. S. Public Health Service, Public Health Bull.,* No. 114: 1–33, figs. 1–32. 1921.

This is a paper of notable value from the standpoint of human as well as of fish ecology. *Gambusia* has been used for some years in malarial control (the fish feeds on both larval and adult mosquitoes), but until now no satisfactory study of the biology or economics of the procedure has been made. Both the habitat relations and the food of *Gambusia* and other top-minnows are considered in reference to the availability and value of these fishes in mosquito control. The author holds that, as a whole, the use of these fishes in malarial control has superior elements of economy and permanent success as compared with other methods employed. The limitations of the fish method of control, however, are not overlooked. C. L. Hubbs.

**Howell, A. H.** A biological survey of Alabama. I. Physiography and life zones. II. The Mammals. *U. S. Dept. Agr., Bur. Biol. Surv.,* N. Amer. Fauna, No. **45**: 88 pp., 10 figs., 11 pls. 1921.

The principal natural physiographic divisions of Alabama are: Mountain region, Tennessee Valley, Warrior Basin and Tableland, Central Prairie Belt, Coast Pine Belt, and Coast Plain or Gulf Strip. Characteristic mammals, birds, and plants are listed only for the Gulf Strip. The distribution of the Upper Austral and Lower Austral life zones in the state is mapped and lists are given of characteristic mammals, birds, and plants of each zone. Many notes on the habits and life-histories of the mammals of the state are given. L. R. Dice.

**Hubbs, Carl L.** The bionomics of *Porichthys notatus* Girard. *Amer. Nat.,* **54**: 380–384. 1920.

Describes the fall and winter migrations of this marine fish; the breeding habitat on rocky shallows within tide limits; the food; the breeding behavior of the male in watching the eggs attached to walls of rock cavities; the protective behavior of the fish

[1] Reprints of Zoological Abstracts, printed on one side for pasting on cards, may be secured from the Business Manager of Ecology, Brooklyn Botanic Garden, for twenty-five cents per volume of four issues.



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in covering itself with sand when disturbed, and attempting to inflict wounds with the opercular spine on being touched. Of interest also is the discussion of the phosphorescence and of the sounds produced by the fish. T. L. HANKINSON.

**Hubbs, Carl L.** The ecology and life-history of *Amphigonopterus aurora* and other viviparous perches of California. *Biol. Bull.*, 40: 181–209, 5 figs. 1921.

The viviparous perches, Embiotocidae, are considered especially in regard to their viviparity and life-histories. Growth as shown by scale structure is prominently considered. Data are given on habitat preferences, and also on the correlation of teeth and intestine with food and of color pattern and other features with habitat. T. L. HANKINSON.

**Klugh, A. Brooker.** A correction concerning the life zones of Canada. *Biol. Bull.*, 41: 272–275, 1 fig. 1921.

On the basis of the distribution of the mammals, birds, and plants, the boundary between the Canadian and Transition life zones in southern Ontario is determined and mapped. L. R. DICE.

**Naumann, Einar.** Spezielle Untersuchungen ueber die Ernährungsbiologie des tierischen Limnoplanktons. *Lunds Universitets Arsskrift*, 17, No. 4: 3–27, 15 figs. 1921.

The kinds of food eaten by *Cladocera*, the methods of obtaining their food and the rate of consumption are discussed. The renewal coefficient for the alimentary canal ranged from a minimum of 15 minutes in four species to 20–30 minutes in *Daphnia longispina*, and to a maximum of 60 minutes in *Sida crystallina*. C. JUDAY.

**Needham, J. G.** Burrowing mayflies of our larger lakes and streams. *Bull. Bur. Fish.*, 36: 269–292, 13 pls. 1920.

Seasonal distribution, life-histories, food relations, and habits of the burrowing mayflies, with special reference to the Mississippi River in the vicinity of Fairport, Iowa. P. S. WELSH.

**Nichols, Estes.** Climate and its relation to acute respiratory diseases. *Mon. Weather Rev.*, 48: 499–501. 1920.

Climate had little to do with the late influenza epidemic. Overcrowded army barracks and the congestion of the civil population, together with the inadequate ventilation made necessary by the shortage of fuel, had most to do with the production of the pandemic. When large numbers of persons are congregated together indoors there is necessarily a heavy concentration of bacteria-laden air, and it appears that a certain concentration is necessary for the spread of some respiratory diseases. With the coming of summer and the opening of windows the germ-laden air is diluted and respiratory diseases diminished. L. R. DICE.

**Tschugunoff, N. L.** Ueber das Plankton des nordlichen Teiles des Kaspisees. *Arbeiten der Biologischen Wolga-Station*, 6, No. 3: 109–162, 1 plate. 1921.

Ninety-two species of plankton organisms were found in the northern part of the Caspian Sea, of which 52 species were fresh-water forms. Of the total number of species, 42 were Rotifera, 26 Cladocera, and 20 Copepoda. This portion of the Caspian Sea possesses three zones, namely, a fresh-water zone with less than 0.75 gr. of Cl per liter, a brackish zone with a maximum of slightly more than 3 grams per liter, and a marine zone ranging from about 4 grams up to almost 16 grams of Cl per liter. The distribution of the various plankton organisms in these zones is discussed. C. JUDAY.

**Wesenberg-Lund, C.** Contributions to the biology of the Danish Culicidae. *Kgl. Danske Vidensk. Selsk. Skrifter, Naturv. og Math.*, Afd. 8, 7, No. 1: 1–210, 21 pls., 19 figs. 1921.

An interesting account of the biology of 25 species of Danish Culicidae. Particular attention is given to the habits and habitats of the larvae. C. JUDAY.

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# NOTES AND COMMENT

### PROPOSED ROOSEVELT-SEQUOIA NATIONAL PARK.

One of the most important pieces of National Park legislation now before Congress is the Barbour bill, H. R. 7452, by which it is proposed to create, from lands which are now partly in a National Park, but more largely in a National Forest, the Roosevelt-Sequoia National Park. The boundaries of the proposed park are the result of an agreement between the National Parks Service and the Forest Service. It has been clearly recognized that once an area is made into a National Park it must be kept strictly as such, and the commercial use of whatever resources it contains abandoned. On the other hand the park features must be national in character and sufficient to justify foregoing the resources.

There will be added to the already existing Sequoia National Park 961 square miles of land now in a National Forest, and there will be returned to the National Forest 105 square miles. This represents a large increase in park values. The 105 square miles eliminated contain no scenic features of national importance aside from the redwood groves. There has been some fear that these groves might be cut. Fortunately they will continue under public control, and be protected as effectively as in the past. The Forest Service has always safeguarded points of unusual interest in the National Forests, and is committed to the protection of these trees as being of far more value to the public as monuments of nature's handiwork than as sawn lumber. Of these 105 square miles, between 65 and 75 are open meadows and hillsides not grown with large trees. This area is of much value for grazing, and has been eliminated from the proposed park for that purpose.

The area to be added to the National Park under the Barbour bill contains, besides the superb Tehipite and Kings River Canyons, Mount Whitney and other magnificent peaks, *more publicly owned redwood trees exceeding ten feet in diameter than the area returned to National Forest.* The present Sequoia National Park contains 1,214 such trees, the Roosevelt-Sequoia National Park will contain 1,304, or a net gain of 90 trees, besides those outside the boundaries which will still be protected. Aside from the redwoods, the 961 square miles contain three or four times as much of the main forest belt, at from 4,000 to 9,000 feet elevation, as the area eliminated.

The Barbour bill, since its amendment to exclude water power from the proposed park, has received the active support of the National Parks Committee, on which the Ecological Society, the National Parks Association, and twenty-four other organizations in National Parks are represented.

### A MENACE TO THE NATIONAL PARKS.

On July 6 the United States Senate passed, in the rush of other business, a bill, S. 3159, defining the rights of the Mescalero Apache Indians in their reservation. Woven into this bill were provisions for making into a National Park, to be known as the "All Year National Park," an indefinite number of small isolated spots within the reservation, and three more isolated spots outside. There is no claim that these spots are scenically, or for any other reason, of such *national* character as would justify making them into a National Park. In fact Senator Bursum of New Mexico stated on the floor of the Senate that the bill "is purely local in character and affects only New Mexico." The bill provides that the new "National Park" would be subject to water power, irrigation, grazing, and mining. Thus it not only ignores the essential qualifica-



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tions of a National Park, but threatens those which may be created in future, as well as the existing ones, with commercial encroachments from which the Ecological Society and all other friends of the Parks have struggled to keep them free. These dangerous provisions, which slipped through the Senate under cover of other legislation, should be removed before the bill reaches the floor of the House. The bill has been referred to the House Committee on Indian Affairs. Further details of the measure, including its full text, will be found in the Bulletin of the National Parks Association, number 29, July 26, 1922, which strongly urges the elimination of that part of the bill creating the "All Year National Park."

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# ECOLOGY

VOL. III OCTOBER, 1922 No. 4

## CONDITIONS INDIRECTLY AFFECTING VERTICAL DISTRIBUTION ON DESERT MOUNTAINS

FORREST SHREVE

*Desert Laboratory, Tucson, Arizona*

Differences in altitude carry with them differences in so many of the physical conditions affecting organisms that for many years we will have a rich field for ecological investigation in the study of these conditions, and of the relation in which they stand to the distribution and activities of plants and animals, including man. Dissimilarities in the character of the altitudinal changes, whenever any two separated regions are compared, add still further complexity to the series of problems which is presented by the biota of mountainous areas. The influence of altitude *per se*—that is, of differences in barometric pressure—has been studied by animal physiologists, but has yielded no conclusive results of importance at the hands of plant physiologists. It is the altitudinal differences of insolation, temperature, rainfall, humidity, evaporation, and a score of related conditions that make up what we were formerly pleased to call "the factor of altitude."

The desert areas of the southwestern United States offer an excellent field for the investigation of life and conditions as influenced by altitude, not only on account of the numerous mountains of all orders of magnitude, but also because the region has been so little disturbed by the activities of man. For several years the writer has been engaged in a study of the vertical distribution of plants in southern Arizona, with particular reference to the Santa Catalina Mountains, near Tucson, but with numerous visits to other mountains in Arizona and adjacent States. The principal aim of this work has been to bring together, on the one hand, data regarding the vertical distribution and upper and lower limits of vegetations and characteristic species, and, on the other hand, to determine the altitudinal gradients of some of the physical conditions of greatest importance to organisms. By the correlation of these two sets of data it is possible to determine the limiting groups of conditions with a precision which is at least akin to that secured in a series of cultures grown under controlled conditions.

On an ideal mountain, having the form of a cone, with uniform gradient from base to top, without irregularities of surface, and with identical soil

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throughout, it would be possible to determine very clearly the relation between the vertical ranges of the biota and the equally ideal gradients of conditions. However, under the natural departures from the ideal, it is necessary to make many interpretations of observed phenomena by way of separating the features due to the operation of the normal vertical gradients of conditions, and the features due to local departures from the normal.

The most common manner in which the topographic irregularities of a mountain may cause departure from the ideal vertical distribution of organisms is simply to raise or lower the limits. In all of the desert mountain ranges there is a marked difference in the vegetation of ridges or peaks and of the bottoms of valleys at the same elevation. There is also a striking difference between the vegetation of north and south slopes at all elevations. In both of these cases we have departures from the distribution that would be found on an ideal mountain cone or that actually found on a gently rising plain. It results in the former case in an interdigitation of contiguous zones of vegetation, and in the latter case in producing alternation or inversion of vegetations.

The object of this paper is to describe some other cases in which the variety of the earth's surface so greatly modifies the vertical gradients of physical conditions that dissimilar communities of plants and animals may be found at the same altitude in adjacent localities.

The general character of the vertical zonation of plant and animal life on the desert mountains of the southwest is similar in all of the ranges from the Colorado River eastward to the Pecos. Rising from plains with desert, desert-grassland transition, or grassland vegetation, the altitudinal zones may be roughly grouped as desert, encinal (open evergreen oak forest), and forest (chiefly coniferous). In mountains rising from plains of sufficient altitude to bear grassland the desert zone is not found, but encinal occupies the lowest mountain slopes.

The actual elevations at which encinal or forest will be encountered in ascending a desert mountain will depend primarily on whether observation is being made of a ridge or valley, or of a north or south slope. The normal lower limit may be defined as the average of the lowest occurrences on north and south slopes respectively; or in the comparison of different mountains it may be more convenient to contrast the lowest or highest occurrences on slopes of the same orientation, away from the local influence of streams or springs. The lowest occurrence in valleys is an extremely variable datum, as individual forest trees will sometimes descend along streams 3,000 ft. below their lowest north slope occurrence.

After the modifying influence of topographic irregularities has been thus eliminated, the lowest normal occurrence of encinal or forest will be found to depend secondarily on three features: (*a*) the elevation of the plain from which the mountain rises, (*b*) the total elevation that the mountain attains,

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(*c*) the mineralogical character of the mountain and consequent nature of its soil.

As an example of the first of these cases, we may compare the southwest faces of the Santa Catalina and Pinaleno (Graham) Mountains. The basal elevation of the former is 3,000 ft. and the lowest pines and accompanying forest vegetation will be found at about 6,000 ft. The latter range has the same type of rock and soil and a basal elevation of 5,000 ft., and the lowest pines on south slopes are found at 7,800 ft. In other words, the increase of 2,000 ft. in basal elevation has pushed the forest upward about 1,800 in the Pinaleno Mountains. Since these two mountains are only 90 miles apart and almost identical in their orientation, character of rock and soil, and in their general vegetation, it would appear that the lower limit of forest is determined by the same conditions in each case.

It is obvious from meteorological considerations that we should have differences in the gradients of climatic conditions in two mountains of different basal elevation. One of the most important expressions of the conditions which control the lower limitation of encinal and forest is the ratio of evaporation to soil moisture. This ratio has been determined for several elevations in the Santa Catalina Mountains,[1] but it has not been possible to secure figures for the Pinaleno Mountains. Further investigation will doubtless disclose a close identity between the ratios for the lower edges of encinal and forest in the Santa Catalina and Pinaleno mountains, in spite of the difference in the actual elevation of "timber line" in the two.

A related case in which different types of vegetation may be found at the same altitude is to be observed in comparing small mountains with larger ones in close proximity and having the same basal elevation. The smaller mountains will be found to have desert species and to lack encinal species at elevations which are occupied by encinal in mountains of greater total height. On the Santa Catalina Mountains the lowest north slope occurrence of encinal plants is about 4,200 ft., and an open stand of junipers and evergreen oaks covers the south-facing slopes at 5,500 ft., while a closed stand of oaks, juniper, and pinon occupies north-facing slopes at that elevation. Twenty-six miles northwest of the summit of the Santa Catalina Mountains is a small isolated granitic range, Black Mountain, with a basal elevation approximately 500 ft. higher than that of the Santa Catalinas. This mountain attains an elevation of 5,583 ft. On the south face of the summit there are no arborescent representatives of encinal, while the north slopes are occupied mainly by a thicket of *Ceanothus greggii* and the shrubby oak *Quercus turbinella,* together with a few individuals of *Quercus emoryi* and *Q. arizonica* not more than 6 ft. in height (fig. 1 A). The latter are the commonest trees of the encinal and reach a height of 25 to 30 ft. at the same elevation and slope

[1]Shreve, Forrest, "The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors," Carnegie Inst. of Wash. Pubn. 217, 1915, p. 92.

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exposure on larger adjacent mountains. In this comparison it is necessary to deduct 500 ft. from the elevation of Black Mountain on account of its higher basal elevation. We then have a north slope at the equivalent of 5,083 ft. exhibiting the same vegetation that is found at the lowermost edge of the encinal in the Santa Catalinas at 4,200 ft. In other words, the vertical gradient of environmental conditions on Black Mountain is such as to permit desert species to range about 900 ft. higher than they do in the Santa Catalina, El Rincon, Santa Rita, and other near-by ranges of greater elevation, and to push the encinal zone upward for a corresponding distance.

The altitudinal gradients of climatic conditions have not been determined for any of the smaller mountains of southern Arizona. There is strong likelihood that they would not correspond with the gradients for the larger mountains, but would more nearly resemble those that have been worked out from Weather Bureau data for a number of towns in Arizona which are situated at different altitudes in open relatively level country. There is little doubt

FIG. 1. Illustrating desert species reaching a higher elevation on rhyolite than on granite. *A*, low shrubby thicket on the north slope of Black Mountain at 5,500 feet. *B*, Encinal trees on the north slope of the summit of Mt. Fagan at 6,000 feet.

that appropriate instrumentation on the summit of Black Mountain would show it to have less rainfall and higher evaporation than the corresponding altitude in the Santa Catalinas.

In selecting examples to illustrate the influence of basal elevation and total elevation on the absolute altitude of vegetational limits, care has been taken to select mountains for comparison which have the same mineralogical and soil character. This precaution is necessary in view of the importance of the nature of the rock and soil in determining the vertical limits of vegetations when other conditions are alike. The lowest absolute elevations are reached by encinal and forest on gneiss and granite, and desert forms correspondingly attain lower maximum elevations on those rocks and their derived soils. The vegetational zones are higher on basalt, rhyolite, and other volcanics, and—at least with respect to certain conspicuous species—still higher on limestone.

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To illustrate this feature a comparison may be made between Black Mountain, which has already been mentioned, and Mt. Fagan, an isolated outlying summit of the Santa Rita range, situated 63 miles S–S–E of Black Mountain, and having the same basal elevation and a summit altitude of 6,175 ft. Black Mountain is granitic, while Mt. Fagan is formed of rhyolite throughout its upper elevations. The vegetation of the north slopes of Mt. Fagan near the summit is similar to that on the north slopes of the summit of Black Mountain. The evergreen oaks are fewer on Mt. Fagan (fig. 1 B), but attain greater size, and the shrubs form occasional clumps rather than a continuous thicket (fig. 1 A). The two mountains, having the same basal elevation and differing only 592 ft. in elevation, exhibit approximately the same phase of the altitudinal gradient of vegetation on their summits. Such desert types as the cactus, *Opuntia chlorotica,* and ocotillo, *Fouquiera splendens,* reach the summit of Mt. Fagan, but do not attain the lower summit of Black Mountain. In short, the difference in the mineralogical character of

FIG. 2. Open forest of Arizona pine *Pinus arizonica* in Bear Canon, Santa Catalina Mountains, looking west along a north-facing slope at 6,000 feet

the two mountains appears to influence the vertical distribution of plants by about 600 ft. Under identical amounts of precipitation the granitic and rhyolitic soils would differ in penetrability, water-holding power, and in their capacities for losing water by evaporation; and these differences will undoubt-

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edly be found to explain the higher elevations reached by desert plants on volcanic soils as contrasted with granitic ones.

The combined influence of the mineralogical nature of mountains and their total elevation is well exemplified in comparing the north slopes of Mt. Fagan just below the summit, at 6,000 ft., with a north slope on the granitic soil of the larger Santa Catalina Mountains, 34 miles distant (compare figs. 1 B and 2). North slopes bearing vegetation similar to that of the north slope of the summit of Mt. Fagan may be found on the Santa Catalina Mountains 1,800 ft. below the stand of pines shown in fig. 2. From this must be deducted 500 ft. to allow for the difference in basal elevation of the two mountains. This offers some evidence that the separate modifying influences that have been described are additive, since the effect due to the character of the soil is equivalent to about 600 ft. of elevation, and that due to the total elevation of the mountains is about 900, while their combined effect in the case cited is 1,300 ft.

The influence on the vertical limitation of desert species which is exerted by limestone and its derived soil may be clearly observed in the Empire Mountains, a small range 31 miles southeast of Tucson, with a basal elevation of approximately 4,000 ft. and a summit elevation of 5,360 ft. Creosote bush, *Covillea,* reaches its highest elevations on granitic outwash in the Tucson region at about 3,050 ft., occasionally appearing up to 3,500 ft. in small colonies. On the limestone slopes of the Empire Mountains it reaches 4,500 ft. in characteristic dense stands, and occurs infrequently up to nearly 5,000 ft. Ocotillo, *Fouquiera splendens,* ceases to be a characteristic plant of the desert slopes of the Santa Catalina Mountains at 4,600 ft., and the highest isolated individuals are found at 5,600 to 5,800 ft. On the limestone soil of the Empire Mountains it flourishes in great abundance up to 5,000 ft., and on limestone in the loftier Swisshelm Mountains, 48 miles to the eastward and with the same basal elevation, it ascends to 6,700 ft. On volcanic soils its highest observed elevation is 6,175 ft., on the summit of Mt. Fagan.

Appropriate localities have not yet been examined for determining the lowest elevations of encinal and forest on limestone soils, and more extensive and diversified outcroppings must be examined in order to complete our knowledge of the upper limits of numerous desert species that have not yet been detected on that type of soil.

The physical texture of volcanic soils, with the exception of that derived from basalt, is such as to offer a ready explanation of the high elevations reached by desert plants on them, since the coarse texture prevents the retention of moisture and carries the soil moisture conditions of the desert up to elevations at which the rainfall may be 50 percent greater than it is on the desert floor. In the case of limestone soils, however, the texture appears to be favorable to the retention of moisture, and the causes underlying the high altitudinal limits of desert species on these soils requires investigation.

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# THE EFFECT OF CLIMATE ON THE EFFICIENCY OF THE PEOPLE OF THE RUSSIAN FAR EAST

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One of the greatest achievements of the new science of climatology is the establishment of the so-called optimum. This principle, first developed for the vegetable kingdom, Ellsworth Huntington has applied to man, and has endeavored to find the optimum for his physical life and mental work, and for his efficiency. The present article is an attempt to apply Huntington's findings to the Russian Far East and its population.[1]

The chief climatic factors influencing man's efficiency Huntington recognizes as (1) the mean temperature month by month; (2) the variability of the weather from day to day; (3) the frequency of storms; (4) the relative humidity. Besides these, the author thinks there should be added the length of the seasons, the intensity and the amount of sunlight, and the electrical conditions of the air.

We shall consider first the temperature. As much space has elsewhere been given to the general monthly and annual temperatures,[2] we shall here turn to the question of most immediate interest, namely, the influence of temperature on human efficiency. On the basis of the work of thousands of factory operatives and students, Huntington came to the conclusion that these workers showed the greatest efficiency at approximately 15° C. (59° F.), and to this temperature he attributes a rating of 100 percent. The temperature above 15° C. grows progressively worse for efficiency, reaching, for example, at 30° C. a rating of only 92.5 percent. Similar results follow when the temperature falls below 15°; conditions become progressively more unfavorable, and when the temperature has reached —20° C., for example, the percentage of efficiency is only 93.6 percent.

[1] Among the scientists of the world who have been at work on the solution of the problem of temperature conditions, those of Russia and the United States occupy foremost places. Of the Russians must be mentioned such men as Voeykov, Brownov, Klossovsky, and others, and among Americans Abbe, H. Arctowski (Polish by birth) R. De C. Ward, J. Warren Smith, J. B. Kincer, A. D. Hopkins, C. F. Brooks, H. Moore and others.

Among Huntington's numerous works see especially his "Climate and Civilization" Yale University Press, and his and Cushing's "Principles of Human Geography" John Wiley and Sons, 1921.

[2] Novakovsky, Stanislaus, "Climatic Provinces of the Russian Far East in Relation to Human Activities," Geographical Review, vol. 12, No. 1, pp. 100–115, 1922.

"The Probable Effect of the Climate of the Russian Far East on Human Life and Activity," ECOLOGY, vol. 3, No. 3, pp. 181–201, 1922.



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TABLE I. *Human efficiency based on average temperature*

| Stations | Latitude | Jan. | Feb. | Mar. | April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Novo-Mariinsk | 64° 45′ | 93.4 | 93.3 | 93.6 | 94.2 | 95.7 | 98.0 | 99.4 | 99.0 | 97.7 | 95.3 | 94.8 | 93.5 | 1,147.9 |
| Markovo | 64° 45′ | 93.0 | 93.1 | 93.5 | 94.1 | 97.1 | 99.2 | *99.9* | 99.2 | 97.4 | 94.7 | 93.6 | 93.3 | 1,148.1 |
| Ghizhighinsk | 62° 4′ | 93.2 | 93.3 | 93.8 | 94.6 | 96.2 | 98.8 | 99.6 | 99.4 | 98.0 | 94.9 | 94.0 | 93.5 | 1,149.3 |
| Okhotsk | 59° 21′ | 93.4 | 93.4 | 94.0 | 95.1 | 96.8 | 98.3 | 99.6 | 99.6 | 98.8 | 95.7 | 94.1 | 93.5 | 1,152.3 |
| Ayan | 56° 28′ | 93.7 | 93.6 | 94.6 | 95.9 | 97.4 | 98.6 | *99.9* | *99.9* | 99.4 | 96.2 | 94.6 | 93.9 | 1,157.7 |
| Nikolaevsk | 53° 8′ | 93.3 | 93.6 | 94.3 | 95.9 | 97.7 | 99.4 | 99.7 | *99.9* | 99.6 | 97.1 | 94.6 | 93.6 | 1,158.7 |
| Petropavlovsk | 52° 53′ | 94.4 | 94.4 | 94.9 | 95.9 | 97.4 | 98.6 | 99.4 | 99.6 | 99.2 | 97.7 | 95.9 | 95.1 | 1,162.5 |
| Alexandrovsk | 50° 54′ | 93.6 | 93.9 | 94.5 | 96.2 | 98.0 | 99.2 | *99.9* | *99.9* | 99.6 | 97.7 | 95.3 | 94.2 | 1,162.0 |
| Blagoveschensk | 50° 16′ | 93.3 | 93.6 | 94.6 | 97.1 | 99.2 | 99.3 | 97.9 | 98.9 | 99.8 | 96.8 | 94.5 | 93.6 | 1,158.6 |
| Khabarovsk | 48° 28′ | 93.4 | 93.6 | 94.6 | 97.4 | 99.4 | 99.7 | 97.9 | 98.4 | 99.8 | 97.7 | 94.7 | 93.7 | 1,160.3 |
| Ekaterino-Nikolskaya | 47° 25′ | 93.6 | 94.0 | 94.6 | 97.4 | 99.4 | 99.7 | 97.9 | 98.4 | 99.8 | 97.7 | 95.1 | 93.9 | 1,161.5 |
| Nikolsk-Ussuriisk | 43° 47′ | 93.6 | 94.0 | 95.3 | 98.0 | 99.6 | 99.6 | 98.4 | 97.9 | *100.0* | 98.3 | 95.5 | 94.1 | 1,164.3 |
| Vladivostok | 43° 7′ | 94.1 | 94.5 | 95.7 | 98.0 | 99.2 | *99.9* | 98.9 | 97.9 | 99.7 | 99.0 | 96.2 | 94.6 | 1,167.7 |
| Possiett | 42° 39′ | 94.4 | 94.7 | 95.7 | 98.0 | 99.4 | *100.0* | 98.9 | 97.4 | 99.7 | 99.0 | 96.8 | 94.7 | 1,168.7 |
| New York | 40° 43′ | 96.2 | 96.2 | 97.4 | 99.0 | *100.0* | 98.4 | 96.9 | 97.4 | 98.9 | 99.8 | 98.8 | 96.8 | 1,175.8 |
| London | 51° 34′ | 97.7 | 97.7 | 98.0 | 98.8 | 99.6 | *100.0* | 99.7 | *99.9* | *99.9* | 99.2 | 98.3 | 97.7 | 1,186.5 |
| Tokyo | 35° 41′ | 95.7 | 97.7 | 98.6 | 99.8 | *99.9* | 97.9 | 96.4 | 95.9 | 97.4 | *99.9* | 99.2 | 98.0 | 1,176.4 |

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In his "Climate and Civilization," Huntington gives a table which shows the percentage of human efficiency at different temperatures. The author has applied these figures to the determination of the efficiency of the people of the Russian Far East, with the results shown in the following table:

In this table are given first the ratios of efficiency by separate months, and at the end their total annual sum. If there were always the ideal temperature which produces the efficiency of 100 percent, the total annual sum would be 1,200. We shall consider this number as a standard in studying the climatic conditions of the various localities of the Russian Far East. When we analyze these tables, we find that whereas in such large centers as London, New York, and Tokyo the total annual figures for efficiency are respectively 1,187, 1,176 and 1,176, in the Russian Far East the figures vary between the limits of 1,147 at Novo-Mariinsk and 1,169 at Possiett. If the temperature alone could determine human efficiency, it will be seen that in the Russian Far East the northern part of the country would rank with the countries having a medium efficiency, and the southern part with those having a high efficiency. But since there are other conditions to be taken into consideration besides the temperature, the resulting percentage of efficiency will actually be much lower than these comparatively high figures. The individual month, which best fulfills the requirements for efficiency in the extreme north is July; in the east, it is August; in the west and southwest, September; and in the extreme south, June. If we compare these findings with conditions in the largest centers of population in the world, we shall notice that in London the best month in this respect appears to be June; in New York, May; and in Tokyo, May and October to an equal degree.

In regard to the amount of variation in temperature, we may say that at most points of the Russian Far East there are small variations from year to year, whereas the daily range (amount from day to night) is considerable, as appears in the following table:

TABLE II. *Average daily range of temperature, Degrees C.*

| Station | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vladivostok | 6.3 | 8.7 | 6.4 | 5.3 | 4.8 | 4.8 | 4.5 | 4.6 | 5.6 | 5.9 | 6.4 | 6.5 | 5.8 |
| Nikolsk-Ussuriisk | 11.8 | 14.3 | 8.2 | 12.7 | 12.9 | 6.3 | 8.9 | 8.8 | 10.3 | 12.4 | 8.2 | 12.5 | 10.6 |
| Blagoveschensk | 8.6 | 11.2 | 10.8 | 7.0 | 10.1 | 8.3 | 8.3 | 7.9 | 10.2 | 9.3 | 8.6 | 9.2 | 9.1 |
| Khabarovsk | 6.4 | 8.0 | 8.1 | 6.0 | 7.3 | 5.5 | 5.8 | 5.5 | 5.8 | 6.1 | 6.0 | 6.8 | 6.4 |
| Cherniaevo | 10.9 | 13.4 | 16.3 | 10.3 | 11.7 | 11.1 | 9.6 | 11.0 | 11.5 | 11.7 | 9.2 | 10.3 | 11.4 |
| Bomnak | 9.1 | 9.5 | 12.9 | 11.1 | 9.7 | 7.4 | 10.5 | 9.8 | 9.1 | 9.5 | 10.4 | 8.7 | 9.8 |
| Nikolaevsk | 7.1 | 11.7 | 10.8 | 11.4 | 6.4 | 6.1 | 8.3 | 8.1 | 8.6 | 9.0 | 8.3 | 8.8 | 8.7 |
| Okhotsk | 4.4 | 7.2 | 13.7 | 13.0 | 4.9 | 3.8 | 3.1 | 4.6 | 5.4 | 4.5 | 4.2 | 4.1 | 6.1 |

In general, we may conclude that the variations are greater in the cold period than in the warm. We shall now consider the variability of the tem-

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perature from day to day. The following table gives a summary of the average variability by months:

TABLE III. *Average interdiurnal variability of temperature, Degrees C.*

| | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vladivostok | 2.9 | 3.5 | 2.1 | 0.8 | 2.3 | 1.4 | 1.6 | 1.2 | 1.3 | 2.9 | 2.9 | 3.8 |
| Khabarovsk | 1.9 | 3.4 | 2.4 | 1.8 | 2.0 | 1.8 | 1.3 | 1.6 | 1.5 | 2.9 | 4.4 | 3.7 |
| Blagoveschensk | 2.3 | 3.5 | 2.8 | 1.7 | 1.9 | 2.0 | 1.4 | 1.6 | 1.6 | 2.4 | 3.4 | 4.2 |
| Bomnak | 1.9 | 2.5 | 1.9 | 2.1 | 1.9 | 2.0 | 2.3 | 1.7 | 1.6 | 2.6 | 4.2 | 3.0 |
| Alexandrovsk | 2.6 | 3.9 | 2.2 | 2.5 | 2.0 | 1.9 | 2.0 | 1.5 | 2.2 | 3.3 | 3.7 | 4.4 |
| Nikolaevsk | 3.9 | 3.6 | 2.7 | 2.0 | 1.9 | 2.5 | 2.2 | 1.8 | 2.0 | 2.4 | 3.0 | 3.8 |
| Okhotsk | 3.0 | 2.8 | 2.9 | 2.3 | 1.5 | 1.4 | 1.0 | 1.0 | 0.7 | 1.7 | 1.5 | 2.1 |
| Petropavlovsk | 3.3 | 3.0 | 2.1 | 1.2 | 1.6 | 1.7 | 1.3 | 1.5 | 1.1 | 1.6 | 1.4 | 2.3 |
| Kluchevskoye | 4.0 | 5.2 | 2.6 | 1.4 | 1.3 | 2.3 | 1.6 | 1.0 | 1.3 | 1.8 | 2.3 | 5.4 |
| Nikolskoye | 1.9 | 2.0 | 1.1 | 1.3 | 0.9 | 0.7 | 0.6 | 0.7 | 0.9 | 1.5 | 2.3 | 3.1 |
| Markovo | 4.9 | 5.8 | 3.4 | 2.2 | 2.4 | 1.8 | 1.9 | 1.5 | 1.4 | 3.5 | 5.3 | 6.7 |

This table shows clearly that the variations from day to day are much less than from day to night. Nowhere except in the most northern point, Markovo, do they exceed 4°, the degree of variation under which Huntington's factory operatives worked most rapidly, and at most points the variation is much below this. In order to understand this matter more clearly, the following table has been prepared to show the number of days when the average temperature of one day differed from that of the next by certain specified amounts during the year 1915:

TABLE IV. *Frequency of days with different degrees of interdiurnal variability*

| Station | Less than 2° | 2°–4° | 4°–6° | 6°–8° | 8°–10° | 10°–12° | More than 12° |
|---|---|---|---|---|---|---|---|
| Vladivostok | 205 | 100 | 33 | 18 | 2 | 4 | 2 |
| Khabarovsk | 199 | 97 | 43 | 13 | 5 | 5 | 2 |
| Blagoveschensk | 195 | 100 | 46 | 14 | 5 | 4 | 0 |
| Bomnak | 190 | 104 | 42 | 18 | 6 | 2 | 2 |
| Nikolaevsk | 171 | 118 | 47 | 15 | 7 | 4 | 2 |
| Alexandrovsk | 187 | 98 | 49 | 14 | 7 | 6 | 3 |
| Okhotsk | 238 | 88 | 28 | 7 | 0 | 2 | 1 |
| Petropavlovsk | 239 | 79 | 31 | 11 | 4 | 0 | 0 |
| Kluchevskoye | 200 | 94 | 32 | 16 | 13 | 3 | 6 |
| Nikolskoye | 284 | 55 | 21 | 4 | 0 | 0 | 0 |
| Markovo | 162 | 101 | 40 | 23 | 18 | 10 | 10 |

We see, therefore, that on the greatest number of days the variation does not amount to more than 2°, and the second largest number of days is that on which the variations run from 2° to 4°, although everywhere there are nearly twice as many days in the first group as in the second. The greatest variation in this year, 1915, was observed in Markovo, and amounted to 23.2 between January 22 and January 23.

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On the basis of extensive observations, Huntington considers that for ideal climatic conditions there should be a variability of 3° or 4°. The Russian Far East, according to this estimate, appears somewhat unfavorable, although as a matter of fact the variability of few parts of the world is much greater. Nevertheless the variability here is not so helpful as it might be otherwise, for only in small measure does it arise from cyclonic storms. Moreover, the smallest variations are observed in the summer when variability is most needed, and the greatest number occur in the cold season when extremes may do harm. As such variations in the winter do not usually exceed 6°, however, they should not be considered very injurious either to the health or the efficiency of the people. On the contrary, the lack of variability in the summer creates, with the generally high temperatures in the Amur and Ussuri regions, a monotony which presumably reduces the percentage of efficiency. But these conditions which are unfavorable for efficiency are very favorable for vegetation, and thus nature compensates the people to some extent. In the Amur and Maritime provinces are found many southern plants which usually require high summer temperatures. During the summer the great humidity and low variability create conditions very much like those of the conservatory, and, thanks to such conditions, many of the southern plants pass through the various stages of their development in a much smaller number of days than they do in the dry atmosphere and under the more marked variability of Turkestan, and some localities of America.

In addition to what has been said above, we must still explain the degree of departure from the ideal climatic conditions. Huntington has found that the ideal outdoor temperature for indoor physical activity appears to be 17° C., and for mental activity indoors about 6° C. He considers that below —3° C. a further reduction of temperature has a negligible effect on efficiency. Basing our calculations on such principles, it is easy to determine the average departures from the ideal conditions for both kinds of activity together. Considering the monthly mean temperatures on the basis of these principles, we may arrange our results in the following table:

TABLE V. *Annual average departure from ideal temperature for mental and physical activity*

| | | | | | |
|---|---|---|---|---|---|
| Novo-Mariinsk | 142 | Petropavlovsk | 123 | Vladivostok | 115 |
| Markovo | 140 | Alexandrovsk | 121 | Possiett | 115 |
| Ghizhighinsk | 138 | Blagoveschensk | 127 | New York | 104 |
| Okhotsk | 134 | Khabarovsk | 123 | Tokyo | 102 |
| Ayan | 129 | Nikolsk-Ussuriisk | 119 | London | 74 |
| Nikolaevsk | 125 | | | | |

Many of the points in the Russian Far East, therefore, show very large departures from the ideal climatic conditions for human activities in comparison with London, New York, and Tokyo. Conditions are especially unfavor-

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able in the northern part, Markovo and Novo-Mariinsk (Chukotsk-Anadyr region). Such points as Vladivostok, Possiett, and Nikolsk-Ussurriisk, in the southern part, may be mentioned, but they are much more favorable, and to a considerable degree approach the standing of New York and Tokyo. In view of this condition, we may expect that the climatic conditions of the section in question will favor the efficiency of the population, and we may look forward to a much higher form of civilization among the natives of this section.

The humidity of the Russian Far East presents marked variations from month to month, and has not that comparative uniformity which is observed in many points of the United States. The optimum for the humidity is established by Huntington as 80 percent at a temperature of 17° C., or about 5 grains of moisture per cubic foot of air. A large departure, whether in winter or summer, appears to be very injurious to health and efficiency. A good example is Tokyo, where during August and September the death rate is very high. These are the months having the maximum temperature and the maximum relative humidity. Although in the territory of the Russian Far East the maximum humidity comes somewhat earlier, it still falls within the warm months. This can not be considered favorable for the activity, efficiency, and health of the population. The comparative relative humidity is shown in the following table:

TABLE VI. *Comparative relative humidity*

| Station | I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | Yr. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Vladivostok | 67 | 61 | 64 | 68 | 71 | 85 | 86 | 86 | 77 | 73 | 64 | 58 | 72 |
| Nikolsk-Ussuriisk | 77 | 82 | 71 | 64 | 65 | 84 | 82 | 86 | 83 | 79 | 77 | 74 | 77 |
| Khabarovsk | 75 | 76 | 66 | 65 | 58 | 73 | 77 | 77 | 76 | 64 | 70 | 71 | 71 |
| Nikolaevsk | 79 | 82 | 79 | 76 | 76 | 73 | 78 | 78 | 76 | 68 | 74 | 72 | 76 |
| Alexandrovsk | 79 | 83 | 72 | 74 | 75 | 78 | 80 | 79 | 80 | 62 | 69 | 76 | 76 |
| Blagoveschensk | 69 | 69 | 56 | 50 | 48 | 71 | 68 | 76 | 74 | 60 | 74 | 81 | 66 |
| Okhotsk | 73 | 72 | 75 | 84 | 86 | 90 | 89 | 95 | 91 | 70 | 65 | 63 | 80 |
| Petropavlovsk | 73 | 77 | 66 | 80 | 71 | 88 | 92 | 90 | 81 | 66 | 65 | 69 | 77 |
| Markovo | 80 | 78 | 76 | 74 | 76 | 71 | 78 | 77 | 85 | 95 | 93 | 91 | 81 |
| Nikolskoye | 83 | 91 | 86 | 89 | 87 | 89 | 94 | 90 | 84 | 80 | 79 | 79 | 86 |
| Tokyo | 64 | 62 | 68 | 74 | 76 | 82 | 83 | 82 | 83 | 80 | 74 | 66 | 74 |
| New York | 78 | 78 | 77 | 72 | 75 | 74 | 76 | 71 | 68 | 64 | 66 | 72 | 73 |
| Washington, D. C. | 77 | 73 | 67 | 66 | 69 | 72 | 65 | 70 | 68 | 67 | 71 | 74 | 70 |

In addition to the factors enumerated above, Huntington also takes into consideration the degree and force of storms which influence both the variability, the temperature, and subsequently the efficiency of the people. According to Kullmer's scale, the Russian Far East is related to the region of slight storminess. In general, the eastern part of European Russia and western Siberia are visited by cyclones very rarely, and they are still more rare in the interior of eastern Siberia and in the Russian Far East. This is

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explained by the fact that, although the tropical cyclones pass into middle latitudes, when they reach the Japanese shore they change their northern direction and move toward the east. The beneficial effects of this factor are therefore less than, for example, in the United States, western Europe, and Japan. We have not the necessary data to give the exact number of cyclones occurring within the territory of the Russian Far East, but will give what information we possess. In Nikolsk-Ussurriisk during the year 1905 the following number of cyclones was reported:

TABLE VII. *Cyclonic storms at Nikolsk-Ussuriisk in 1905*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| January | 4 | April | 4 | July | 4 | October | 3 |
| February | 4 | May | 6 | August | 2 | November | 3 |
| March | 2 | June | 3 | September | 6 | December | 3 |
| | | | | | | Year | 44 |

Out of these 44 cyclones, the centers of only 9 passed over Nikolsk-Ussurriisk, or to the northwest of that place. They gave rise to three strong snowstorms, two long periods of rain, and four heavy rains with floods. The rest passed southeast of Nikolsk-Ussurriisk and were not of such a stormy character. Often the cyclones are followed by anticyclones, accompanied by high barometric pressure and a heavy drop in temperature. In general, the cyclones cover only the southern part of the Maritime provinces. In the Okhotsk and Bering seas, however, covering the northeastern part of the Russian Far East, cyclones are observed more frequently and are of a very stormy character. Thus, although insufficient data make it difficult to record the degree to which the comparative absence of cyclonic storms reduces human efficiency, nevertheless it may be concluded that the Russian Far East can not in this respect be placed on the same level with central and eastern United States, Europe, and Japan, where the most intensive cyclonic regions are observed and where simultaneously the people show more vigor.

In the matter of the amount of sunshine, when we compare the Russian Far East with those countries which have sometimes too much sunshine and at other times too little, we may conclude that these extremes have an injurious influence on human efficiency, causing chiefly various nervous disorders and a general weakening of the will-power. Although at the present stage of the science of climatology we can not establish the optimum sunshine for efficiency, we may venture the opinion that under the most favorable conditions there should be about 60–65 percent of the possible sunshine in the summer period and 75–80 percent in the winter, making an annual average of 65–70 percent. Many localities of the Amur, Nikolaevsk, and Ussuri regions approach these conditions very closely. Only a few of them in the summer time, particularly in July, have a considerably lower percentage. In any case, it should not be thought that the population of these regions suffers any considerable reduction of its efficiency because of these conditions. But in the

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northern part of the Okhotsk, Kamchatka, and Chukotsk-Anadyr regions the percentage of sunshine is much smaller, and the population shows an inclination to nervous diseases, which reflect very harmfully on its efficiency.

The author thinks that among the factors influencing human efficiency the duration of the seasons should also be recorded. Huntington's reason for not taking this into consideration is quite clear. His attention was fixed on the United States and other countries where the seasons change one after another regularly, and where the winter is not of such great length as it is in many localities of the Russian Far East. The winter in parts of this territory lasts from 6 to 9 months, and undoubtedly this extended monotony lowers energy and efficiency. Life in the northern and northeastern regions of the Russian Far East breaks up into two irregular periods—a period of navigation and fishing (summer) and a period of stagnation (winter). The life of the local population is revived about the time of the first appearance of the boats on the waters. Then begins a new and very short season, lasting altogether from 3 to 4 months. During this period the people must do all that is done in other places during the whole year. Thus they work nervously, even through the night, not allowing themselves either rest or pleasure. The busiest are those whose work is connected with navigation, but hardly less busy are the fishermen. The fish, particularly the salmon, are quite capricious. They pass in definite periods and the fishermen must watch for their appearance. The least carelessness may spoil the whole catch. Rapid preparations must be made before the appearance of the fish, such as building camps, putting the tackle in order, preparing the barrels, etc. When everything is ready, whole days and nights must be spent in working with the fish—catching, sorting, salting, drying, packing, etc. Such nervous work undoubtedly has an injurious effect upon the mental state, health, and efficiency of the people. The gold-miner also has to do a great deal of work in a very short time.

In general, then, in the summer time all the population works abnormally, strenuously, and above its strength. But when the last whistle of the boat is heard, life changes its aspect entirely. A long period of stagnation begins, when many localities are cut off entirely from the outside world, and the days drag on long and monotonous. Such a condition is reflected very harmfully on the population, causing depression, weakening of will-power, and paralysis of efficiency. For this reason the winter season is marked by a great increase in nervous diseases, as well as in drinking and immorality. History gives many instances of the corrupting effect of climatic conditions in the Okhotsk, Kamchatka, and Chukotsk-Anadyr regions. Ambitious and talented young officers who were sent into these sections found the monotonous winter and the complete separation from the civilized world so unbearable that, in spite of their fine education and lofty ambitions, they fell into drinking, corrupt living, and the commission of bribery and numerous other crimes. In a

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short time they became rough and sordid, and treated the natives under them with great severity. Such circumstances are due not so much to the evil or good inherent in separate individuals as to the untoward climatic conditions, the various extremes, and the monotony of it all. It may be said without exaggeration, therefore, that the length of the seasons, especially their irregularity and monotony, have a very injurious effect on the mental condition, the energy, and the efficiency of the population.

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# PRESERVATION OF NATURAL AREAS IN THE NATIONAL FORESTS[1]

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Biologists and those interested in allied lines are familiar with the movement launched by the Ecological Society to secure the preservation of so-called natural areas where plant and animal life and natural features in general may remain undisturbed by human activities. In seeking such conditions one naturally turns to localities remote from established communities. The National Forests hold out much promise because they contain large sections which as yet are but little affected by industrial development, and because they are under Federal control. The writer has been requested by the chairman of the "Committee on Preservation of Natural Areas" of the Ecological Society to list the National Forests of Arizona and New Mexico as areas which will remain at least in a semi-natural state.

Within these two States are 15 National Forests, whose combined area is nearly 22 million acres. Vegetation zones range from desert or semi-desert at from 3,000 to 4,000 feet in elevation to alpine conditions above 12,000 feet. With rising altitude, the plant associations pass successively from desert grasslands to brushlands, woodlands, yellow pine forest, Douglas fir-white fir forest, Engelmann spruce forest, and finally to treeless areas above timberline. The two extremes of desert and timberline do not often occur within the boundaries of the same forest, although this is the case in several instances.

It is of interest to consider in what measure the National Forests under the existing methods of management will answer the requirements for "Natural Areas." The general policy governing the handling of National Forests is that of highest use to the public. The primary purpose is the production of timber. This implies that when a forest crop is mature it will be harvested. Associated with timber production is the utilization and development of grazing, agriculture, water, mining, recreation, and other resources.

Cutting disturbs natural forest conditions in a degree which varies with the type of forest and with the method of management. Under all systems of management practiced in the Southwest, natural reproduction is the first consideration. Mature and over-mature trees are removed unless needed for seed production, shelter to seedlings, or to control streamflow and erosion. Between the seedling stage and the mature stage are considerable numbers of thrifty young trees which will be ready for cutting before the seedlings reach

[1] Read before the second annual meeting of the Southwestern Division of the American Association for the Advancement of Science.



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maturity. Under no circumstances is removal so heavy as to destroy what may be termed forest conditions. Cutting does, however, disturb the natural balance prevailing in the virgin forest. This results, at least temporarily, in abnormal development of herbs and shrubs as well as of the trees themselves. Under proper management, the trend of development after cutting will be toward restoration of the virgin conditions. In what measure this end will actually be attained, however, can not be foretold.

Next to cutting, the most important factors are fire and grazing. The devastation of vast areas, as exemplified by old burns in the high mountains, is not likely to be repeated. Fires can not be entirely eliminated, but records show that during the past ten years an average of only two tenths of one percent of the area in the National Forests of Arizona and New Mexico has been burned over each year. In the past grazing has in many instances altered the character of forests by destroying forest reproduction and herbaceous cover. Under forest management these abuses will be practically eliminated. Even under scientific regulation of grazing, however, the composition of herbaceous plant associations will probably not be the same as would be the case if no grazing took place. A strong argument in favor of moderate grazing is that it assists in the control of fires.

With reference to wild animal life, both grazing and human occupancy have a disturbing effect. Each class of stock more or less repels (or sometimes attracts) certain wild species, and each class of stock changes the habits, food supply, and abundance of predatory animals and hence the balance of non-predatory species. Man, by hunting on the one hand, and by control of predatory species on the other, has a separate effect on the habits and abundance of each species, predatory and non-predatory, but under proper management the net result will probably be an artificially sustained balance in favor of game on most areas.

Road building, which is to a large extent associated with industrial development, stimulates tourist traffic. The effect on vegetation is unimportant excepting in so far as it may increase the prevalence of fires. Wild animal life is subjected to greater disturbance than is plant life. Lawful hunting has less serious consequences than indiscriminate shooting of roadside animals, particularly birds.

Although the general administration of the National Forests safeguards them against destructive exploitation, it does not assure that any areas will be kept in a natural state unless specific provision is made to attain that end. It is true that extensive areas, because of inaccessibility, will remain comparatively immune from exploitation for many years; but this is merely a temporary condition which unforeseen developments may terminate at any time. The only way in which the preservation of natural conditions can be assured is by formal withdrawal of specific areas under specific provisions as to future care.

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This is not a revolutionary idea among professional foresters. The principle of highest use which is the keystone of our National Forest policy recognizes that although the forests as a whole should be devoted primarily to timber production, specific areas may serve the public better in other ways. Certain tracts may be regarded as chiefly valuable for watershed protection; others may be regarded as chiefly valuable for purposes of recreation. Often these special uses are combined with timber production, but this is not always the case. A plea for special recreational areas is voiced by Leopold in an article, entitled "The Wilderness and Its Place in Forest Recreational Policy," in the November (1921) issue of the Journal of Forestry. Leopold would set aside one relatively large area in each State to be maintained in such a condition that it could be truly characterized as a wilderness. Other foresters have expressed a need for reserving typical areas which would remain as examples of the primeval forest after the mass of virgin stands has disappeared.

It is too much to expect the Forest Service to set aside separate areas to satisfy every individual taste, but if all of these interests can be harmonized, there is reason to believe that they can be met. To the true lover of the outdoors, relative inaccessibility by modern modes of travel and the rigid exclusion of all things artificial may seem essential requisites; on the other hand, the scientist who goes into the woods to study rather than to play would welcome a few modern conveniences. Those who are interested primarily in animal life demand large, continuous areas in order to permit the natural movement of animals; those whose chief interest lies in vegetation would prefer a larger number of relatively small areas so distributed as to represent all conditions of altitude, topography, soil, etc. The sportsman wants hunting and fishing; but certain types of nature lovers would protest against the killing of any wild life.

On some points the various conceptions would be wholly incompatible, but on others a compromise would not call for serious sacrifices. The advocates of the "wilderness" idea should be allowed to realize the essential features of their scheme in at least one area in the Southwest. Such an area would also serve most admirably the interests of a large body of scientific workers. A compromise on the road question might be reached by choosing a location well off of main routes of travel, but accessible by roads of the type that can be covered by automobile, though not sufficiently good to attract tourists. Without such transportation facilities, fire protection would be exceedingly difficult. As for hotel accommodations and other modern conveniences within the area, the scientist could reasonably be expected to forego them.

Views differ as to how far restrictions on hunting and fishing should go. Those who would absolutely prohibit these sports probably represent a very small minority who can find the realization of their ideal in National Parks

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and Game Preserves. Hunting with modern methods of game management is probably just as favorable to game preservation as no hunting and no management, if not more so.

One or two areas, even though of large size, would probably not represent a sufficient variety of conditions to satisfy foresters and botanists. Their needs could be met by selecting small supplementary areas of from 80 to 640 acres.

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# THE RECIPROCAL RELATION OF SOIL AND INSECTS[1]

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The soil is an integral factor in the study of many biological problems. The importance of this has been recognized by the agronomist, the botanist, and the chemist. The zoologist, and particularly the entomologist, on the other hand, have not given the soil the consideration necessary to an understanding of many of the fundamental animal activities. This was brought to the writers' attention in connection with a study of subterranean insects which attack the roots of crops; and the present paper, which might be termed a preliminary survey of the field of soil entomology, is an attempt to review some of the work which has been done along this line and to suggest the scope and possibilities of future research. While the literature on soils and soil insects is voluminous, little effort has been made to systematize or correlate the data. It is only within recent years that the entomologist has recognized the fact that the basis of entomological study is insect behavior, which in turn is a response to the influence of the environmental complex. In other words, we now have the application of the principle of cause and effect, and the entomologist is no longer confined to insects, but investigates all factors which influence their activities.

The soil offers a multiplicity of problems which are of direct interest to the entomologist. It is the home of a vast series of insects either during their entire life or some portion of it. It affords shelter and protection to another large group. In addition, being the medium for plant growth, it becomes a factor in the food supply of insects. Distribution, relative abundance, and seasonal activities of insects may be correlated with certain soil conditions. Finally, a knowledge of soils is fundamental to the development of many control measures. On the other hand, while insect life is largely dependent on the soil, there is also a reciprocal relation, since the soil is benefited by the presence of insects.

## The Soil as an Environment

The soil is a complex of many factors which separately and conjunctively are of vital importance to insect life. Jennings (1906) points out that since the environment is a complex of many factors, every animal lives surrounded by and responds to a complex of factors, at least in its normal life activities

[1] Contribution No. 77 from the Entomological Laboratory, Kansas State Agricultural College. This paper embodies some of the results obtained in the prosecution of project No. 100 of the Kansas Experiment Station.



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within its normal complex. In the case of the soil, the more important factors are topography, texture, structure, color, temperature, moisture, evaporation, light, pressure, food, organic matter, materials of abode, nitrogen, carbon dioxide, oxygen, and enemies. Some of these probably are of little importance in the life economy of soil-inhabiting insects, while others exert a tremendous influence. In many cases it is the interaction of a number of factors that must be considered, and soil technology, therefore, becomes a part of many entomological problems in arriving at an interpretation of the behavior and activities of insects in the soil. Lyon and Fippin (1911), in discussing the principles of soil management, present a comprehensive outline of the factors making up the soil environment.

It is not within the scope of this paper to discuss all of the soil problems involved in a study of subterranean insects, but to indicate something of the complexity of the investigations and the results that may be obtained. With soil temperature, for example, it must be considered that the heat of the soil comes from three sources, solar radiation, conduction, and organic decay; that it influences the biological, physical, and chemical constituents of the soil; and that it is dependent on many factors of the soil, such as specific gravity, specific heat, color, topography, conductivity, air circulation, and water content. Water exists in three forms, gravitational water, capillary water, and hygroscopic moisture, the relative amount of each being determined largely by the physical properties of the soil. The amount of air varies with the different types of soil and in any soil is subject to change from time to time. In general, it may be said that the factors influencing the volume of air are texture, structure, organic matter, and moisture.

The food of subterranean insects consists principally of decaying organic matter and micro- and macro-organisms. All of these occur in varying quantities in practically all soils. Decaying organic matter is probably the most important, since it not only furnishes food for a large number of insects, but also influences the number of micro- and macro-organisms. The amount of organic matter present varies greatly with different soils, a conservative average being from two to three percent. The number of micro-organisms, both plant and animal, in the soil is enormous. In some cases it is estimated that an ounce of fertile soil may contain 30,000,000. A large percent of these belong to the plant group and include bacteria, algae, fungi, and slime molds. The macro-organisms consist of the underground parts of plants and the larger forms of animal life.

The practical application of environmental studies is manifold and should lead to a better understanding of the relation of insects to the soil habitat, the distribution of insects, their relative abundance, their behavior, and finally, in the case of injurious species, to the methods of control. Shelford (1911), writing of the distribution and dispersal of animals, states that every animal selects an environmental complex as its general habitat, that the breeding

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grounds are usually the most important index to the true habitat, and that each species is usually distributed as far as its environmental complex extends unless barriers are encountered. In support of these statements, Shelford finds that the factors governing egg deposition of certain species of tiger-beetles (Cicindela) are slope, kind of soil, soil moisture, light, and temperature.

The work of Cameron (1913) shows that gravitational water is the most abundant and most destructive form of moisture affecting insect life within the soil, while capillary moisture is the most favorable. In the case of wire-worms, Hyslop (1915) states that the larvae of the genus *Melanotus* occur in heavy, poorly drained soils, while Anderson (1920) finds that *Horistonotus uhlerii* infests soils that are classified as fine and very fine sand, whose texture and structure are of such a nature that saturation is almost an impossibility.

## Insects of the Soil

It might be stated that in a general way all insects are directly or indirectly dependent on the soil, since it is the basis of all life. On the other hand, there is a vast series of insects directly associated with the soil. A review of the orders of insects from the primitive Thysanura to the highly specialized Hymenoptera indicates that practically all of them are represented in the soil fauna. In the present discussion a brief review is given of the orders of insects, indicating the more important groups which utilize the soil. The list, while not exhaustive, is presented to show the great variation in species and their activities.

*Thysanura and Collembola.*—Especially abundant in the soil, some of the Collembola being found at depths of six feet or more.

*Orthoptera.*—Examples of the soil-inhabiting insects of this order are the Acrididae, which deposit their eggs in the ground; the Phasmidae, which drop theirs on the surface; and the Locustidae and Gryllidae, many of which spend much of their life underground.

*Platyptera.*—This order is best represented by the termites.

*Ephemerida.*—The nymphs of May flies, while they live in aquatic situations, often feed in mud.

*Thysanoptera.*—Numerous species of thrips are found in and on the ground.

*Hemiptera.*—The species of this order are found largely on plants. Certain groups, however, as the Cicadidae and the root-feeding species of Aphididae and Coccidae, are intimately associated with the soil. Other families that might be mentioned are the Galgulidae and Saldidae, which live in mud flats, and the Cydnidae, which burrow in sand. Isolated species of Cercopidae, Fulgoridae, and Membracidae are also encountered in the soil.

*Neuroptera.*—The most striking soil group of this order is the family Myrmeleonidae, the larvae of which construct conical pits in sandy areas for entrapping their prey.

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*Trichoptera.*—These insects, while living in aquatic situations, use sand or soil in some instances for the construction of larval and pupal cases.

*Lepidoptera.*—This large order contains numerous species that live in the soil for varying periods of their life cycle. In many cases only pupation occurs in the soil, the other stages being above ground. This occurs among certain species of Notodontidae, Geometrina, Sphingidae, and Noctuidae. The larvae of many Crambidae live in nests constructed of bits of earth. Some Noctuidae, especially the cutworms, spend much of the larval period in the ground, and in the case of Chorizagrotis eggs are deposited on clods.

*Diptera.*—The larvae and pupae of a large number of families of Diptera are found in the soil, and especially that rich in organic matter. Such families as Tipulidae, Tabanidae, Leptidae, Asilidae, Bombyliidae, Therevidae, Dolichopodidae, Mycetophilidae, and Bibionidae are well represented. In the case of Oestridae the larvae are parasitic on mammals, but leave the host to pupate in the ground.

*Coleoptera.*—The beetles represent one of the largest orders of insects and are especially abundant in and on the ground. Such families as Carabidae, Cicindelidae, Silphidae, and Staphylinidae spend their entire life closely associated with the soil. Nearly all of the Scarabaeidae, Elateridae, Lampyridae, and Meloidae spend the egg, larval, pupal, and part of the adult stage in the ground. Numerous species of other families are well represented in the soil fauna.

*Hymenoptera.*—The ants, bees, and wasps present many interesting groups of soil-inhabiting insects. The Formicina, Sphecina, and many Apina excavate extensive tunnels, burrows, or cavities in which they store food and rear their young. The adults of many species of Scoliidae burrow through the soil, parasitizing other insects. The mason bees and wasps, while not living in the soil, utilize this material in the construction of their nests. The great variety of species and diversity of habits represented by this order make it one of the most important soil groups.

## Abundance of Insects in the Soil

This phase has not been investigated extensively and offers an exceptionally interesting field for research. McAtee (1907) made a census of the animal life in four square feet of soil to the depth a bird could scratch and on the basis estimated that there were 1,216,880 animals, principally insects, in an acre of woodland and 13,654,710 in meadowland. In addition, he found tangible remains of 488,925 dead insects per acre of woodland and 240,030 per acre of meadowland. Morris (1920), reporting on the fauna of permanent pasture in Cheshire, states that "The census of insects actually found in the samples of soil gave an insect population of 3,586,088 per acre. The family best represented in number of individuals was the Bibionidae, species of which made up 32.4 percent of the total number of soil insects. The next

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in number were the Mycetophilidae, 16.7 percent, and the Staphylinidae, 12.2 percent. With regard to the number of species occurring in the soil, the Coleoptera, with 29 species, was the best represented order." Marlatt (1907) records 84 periodical cicada openings to the square foot at Frederick, Maryland, and estimates from 30,000 to 40,000 in the ground surrounding a fairly good-sized tree. According to Packard and Thompson (1921), the larvae of the range crane fly often occur in enormous numbers, as many as 300 occurring in an area of one square foot. McCook (1877) records 1,600 nests of *Formica rufa* forming a single colony containing hundreds of millions of workers. There is no doubt that in areas where ants or termites occur the number of individuals present is enormous. It might also be said that soils rich in organic matter usually contain thousands of Thysanura, Collembola, and immature stages of Diptera.

## Uses that Insects Make of the Soil

The uses that insects make of the soil and the benefits that they derive are almost as numerous and as varied at the groups of insects themselves. It is not within the province of this paper to enumerate all of these, but rather to call attention to the more striking examples. In general, insects may be said to utilize the soil for shelter, protection, materials of abode, food, moisture, air, heat, and as an avenue of travel. The use of the soil for shelter and protection is often temporary, as in the case of those insects which normally live above ground but burrow into it to escape their enemies, to avoid excessive climatic conditions, or to undergo certain metamorphic processes. On the other hand, many species spend their entire life or the major part of it in the soil. Some of these, as the ants and termites, excavate large subterranean cavities, while others, as the solitary bees and wasps, construct a single burrow or cell. In many instances the soil furnishes shelter and protection for only one or two stages in the life cycle. The Acrididae deposit their eggs in the earth, the other stages occurring above ground, while some Noctuidae are found in the soil in the larval and pupal stages. In connection with the utilization of the soil for protection reference might be made to the peculiar markings of some insects which conform to the general ground color. This is strikingly shown in many of the Acrididae and Cicindelidae, while many species of Rhyncophora, when disturbed, often escape detection by falling to the ground and feigning death. Certain Tenebrionidae have the integument of the elytra coated with so dense a crust of indurate earthy matter that it is impossible to remove it and thus it becomes a part of the insect.

There are many insects that do not live in the soil, but use it in the construction of shelters. The mason bees and wasps build elaborate structures of earth for the rearing of young. Some of the Trichoptera, which live in the water, construct larval and pupal cases of sand, and King (1919) has found that the eggs of some Carabidae are placed in cells made of mud and

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attached to plants. The enormous termite mounds of the tropics might be placed in this category.

The soil is a vast storehouse of food that is utilized in various ways by insects and many interesting problems arise in connection with a study of the feeding habits of subterranean insects. Many are free-living, moving from place to place in search of food; some are sedentary, while others leave the soil environment, returning with food material. The ants, for example, store seeds, grow fungus, take care of aphids and coccids, are predaceous on other insects, and at times cannibalistic. The larvae of such groups as Carabidae and Asilidae search through the soil for prey. The ant-lion constructs a conical pit for entrapping its food, while the cicindelid larva waits for its prey at the mouth of its burrow. *Canthon laevis* constructs a ball of manure, which is carried to a suitable place and buried, while *Copris carolina* packs its burrow with dung. The Silphidae diligently bury dead animal matter. The solitary wasps fill their excavations with insects and spiders, while the solitary bees fill theirs with pollen. Many parasitic insects invade the soil in search of hosts. The activities of the adults of the various species of Tiphia and Elis, which parasitize white grubs, might be mentioned in this connection. The moles, gophers, and other rodents are infested with lice and in some cases fleas.

The foregoing is not an attempt to cover the field of the food activities of soil-inhabiting insects, but rather to call attention to the variety of habits and suggest the interesting problems of a study of the food habits. Oxygen, moisture, and heat are all essential to the insect's life economy and are supplied in the soil in varying forms and quantities, determined largely by the interaction of many closely related factors. Although these factors are subject to great variation, many insects adjust themselves readily to the fluctuations. Ants move their immature forms from one chamber to another in order to secure optimum conditions, while wireworms, false wireworms, and white grubs burrow laterally or perpendicularly.

## Modifications and Adaptions for Living in the Soil

Insects have generally been considered of terrestrial origin, and the greatest modifications have been those which have enabled the species to leave this environment. That development has been from a terrestrial habitat is emphasized by the fact that primitive insects are closely related to this environment. Practically all orders and nearly all families are represented in the soil fauna and the simpler forms of metamorphosis occur in those groups which are largely subterranean. The development of wings, compound eyes, and the more highly specialized forms of metamorphosis have enabled many insects to mitigate the conditions existing outside the soil environment. This phase has been discussed by Osborn (1908), who states that primitive insects

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were largely terrestrial in habit, and divergence has been along certain main pathways such as adaptation to underground existence, aquatic life, arboreal life, sedentary conditions, parasitic habit, gall-forming habit, and a host of minor lines of special adaptation. He also points out that the tendency to burrow underground is one of the more primitive lines of adaptation. Certain general modifications might be mentioned as associated with subterranean life. Usually the body is more elongate, the sense organs more highly developed, the eyes and wings reduced or wanting, and metamorphosis simple. While all these modifications do not apply to all soil insects, it may be stated that they are often present in direct proportion to the amount of time the insect lives in the soil.

There are a number of interesting modifications which should be mentioned at this time. Several groups of insects exhibit a striking development of the anterior legs for digging and transporting earth. The mole cricket has the front legs modified, resembling those of a mole, and admirably adapted for shoving dirt aside and also for cutting off roots. The anterior legs of the nymphs of the seventeen-year cicada show a peculiar enlargment of the femora and tibia and resemble the cutting mandibles of biting insects. As pointed out by Marlatt (1907), the anterior tarsus of this cicada undergoes a peculiar metamorphosis in the adolescent life, being modified in accordance with the various activities of the insect. Many of the Scarabaeidae also exhibit various modifications of the anterior legs, the tibia being enlarged and flattened, and in some species the tarsi are reduced or wanting.

Certain larvae possess interesting structures which enable them to live in the soil. One of the most striking of these is the larva of the tiger-beetle, which has a hump-like growth on the back of the fifth abdominal segment. This structure bears a pair of long, curved hooks and a pair of short, vertical spines, together with numerous strong bristles. This outgrowth enables the larva to move freely in its burrow and also to maintain its position at the opening.

## Benefits to the Soil from Insects

While insects utilize the soil in numerous ways and in many cases are dependent on it for their existence, there is also a reciprocal relation, since insects are an important factor in soil formation, renovation, and maintenance. This fact has been overlooked by many entomologists, although generally recognized by soil students. Van Hise (1904) states that animals perform a very important mechanical function in weathering the rocks, in promoting their transportation, and in exposing new surfaces to the weathering forces; and consequently they greatly accelerate denudation and deposition. Shaler (1891) considers the group of results due to the action of organic life very nearly as important as that brought about by the action of water, and in his discussion of organic life much emphasis is placed on insects.

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The importance of insects as beneficial soil agencies may be seen when it is recognized that, with the possible exception of protozoa and nematodes, insects constitute the largest group of the soil fauna. Many species spend their entire life cycle or the greater portion of it below ground, undergoing the vital activities of metamorphosis, growth, feeding, and reproduction in this environment. The larvae of many beetles living in the soil are comparable in their activities to the earthworm which has been discussed by Darwin and others. The methods whereby the soil is benefited by the presence of insect life are too numerous and varied to permit a full discussion at this time. Briefly, these benefits may be considered of a physical and chemical nature and may be classed as interchange of soil, separation of soil, aeration, drainage, and addition of organic matter. Probably the most important activity of insects is that of burrowing through the ground, since this results in the movement of the soil along more or less definite lines and produces an interchange of the subsoil with the upper layer. This phase has not been as fully investigated in the case of insects as it should be. As a parallel, however, Darwin (1883) estimates that earthworms annually bring 18 tons of earth per acre to the surface. Branner (1900), writing of the ants and termites of the tropics, states that the mounds are of great size, numerous, and contain many tons of earth. Shaler (1891) found ants so numerous in a field near Cambridge, Mass., that they transferred enough material each year to cover the surface of the ground with one fifth of an inch of new soil.

In addition to this interchange of soil due to burrowing, the ground is opened up for better aeration and drainage. The data on the extent and distance which insects burrow are very limited. In the case of ants, the galleries and tunnels have been found extending several hundred feet from the nest. In connection with the interchange of soil there is often a separation of the particles. The ants in particular might be mentioned here, since, as pointed out by Shaler (1891), many of them separate the finer detritus from the coarser, placing the finer material on the surface and burying the larger particles.

Another important benefit which the soil derives from insect activities is the addition of organic matter. This is accomplished in numerous ways; one of the most striking and far-reaching is in the case of the interchange of soil. The bringing to the surface of large amounts of earth gradually covers the waste from the aerial parts of plants and incorporates it with the soil. Vegetable matter is also added in large quantities by certain groups of insects which carry plant material beneath the surface. Here, again, the ants are extremely active, although such insects as cutworms and termites might be mentioned. The leaf-cutting ants, which live in large colonies, are capable of stripping a tree of its foliage in a few hours and transporting this material to their nest. Many ants store quantities of seeds in their homes and the solitary bees fill their burrows with pollen.

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Another group of insects represented by the various members of the Scarabaeidae incorporate considerable organic matter with the soil by digging burrows in which they bury manure as food for the larvae. Shaler (1891) states that a single pair of beetles will add several cubic inches to the soil in a year.

While many insects add vegetable matter to the soil, some are active in burying animal matter. The Silphidae should be mentioned especially in this connection, since they bury dead animals by removing the earth, allowing the body to settle until finally it is below the surface. Shaler (1891) states that were it not for such insects the surface of the earth would be covered with a deep layer of bones. Many of the solitary wasps kill or paralyze insects and spiders, which they then place in burrows in the soil.

Several other benefits to the soil might be mentioned. Many insects in feeding underground ingest considerable soil matter and this is acted upon by various body secretions which decompose the inorganic matter and cause certain chemical changes. This material also often undergoes a grinding process in the proventriculus which reduces the soil particles and renders them more susceptible to the active body compounds. This phase has not been investigated in insects, but several workers have conducted experiments along this line with earthworms. The excreta of insects which soon becomes incorporated with the earth is composed largely of active chemical compounds which add much to the soil. Juritz (1920) made an analysis of the droppings of *Antheraea cytherea* and compared it with horse, cow, and barnyard manures. The caterpillar droppings contained a relatively high percentage of potash, and compared favorably with the other manures in their contents of nitrogen, lime, and phosphoric acid. The decomposition of dead insects either above or below ground might also be mentioned, since much is added to the soil in this process. And finally, organic matter already occurring in the soil is rapidly decomposed and made available as plant food by the work of various insects.

## The Relation Between Soil Technology and Insect Control

Economic entomologists, and particularly those engaged in the study of cereal crop insects, are directly interested in soil problems in connection with the development of control measures. Many of the methods advocated for the control of insect pests are dependent on general agricultural activities, which in themselves are closely related to soil conditions. In general, it might be stated that a knowledge of the soil is fundamental in any control measure involving cropping, cultivation, use of soil fumigants, sprays, and repellents.

### *Cropping*

The rotation of crops is one of the more generally recommended control measures for many insects. It is especially valuable for such pests as are

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limited to one food plant or group of closely related plants, or in the case of such species as are slow in dispersal. Rotation, however, can not be practiced successfully unless the soil conditions are definitely known. As Lyon and Fippin (1911) point out, it is a matter of common observation that all crops do not grow equally well upon the same soil. Each plant is adapted to make its best growth on a particular soil and under a particular climate. Any departure from these ideal conditions results in changing the character of the plant and in reducing its value.

### *Cultivation and Handling of the Soil*

The entomologist is often confronted with the problem of developing some cultural system for the control of insect pests. This system may involve such practices as plowing at different seasons of the year, listing, disking, harrowing, cultivation, and summer fallowing. In order to know just how far these operations can be carried out, it is necessary to have a thorough knowledge of the soil, otherwise more harm may be done than good. Soils respond differently under cultivation, and the successful manipulation of the ground is dependent on a knowledge of the important factors involved. Tillage produces a modification of the food, temperature, moisture, air, and texture of the soil. Good cultural management, therefore, involves an analysis of the existing condition of the soil and a determination of the changes to be effected.

### *The Use of Soil Fumigants*

Soil fumigation has recently come into prominence as a method for the destruction of several insects and particularly the grubs of the Japanese beetle. A résumé of the literature indicates that this field of investigation is just beginning. The experimental work will of necessity follow many lines, and soil technology will have an important place. Komp (1920), in outlining the problems connected with a study of soil fumigation with carbon bisulphide, says that it is necessary to determine the maximum dosage noninjurious to the plant, the minimum dosage lethal to the insect, and the influence of temperature and moisture conditions upon the effectiveness of the fumigation. De Ong (1917), writing of sodium cyanide, states that (1) a definite ratio must be established between the minimum point of toxicity to the insects and the maximum dosage which is safe for germinating seeds and plants, and (2) a study must be made of the physical and chemical action of the gas in the soil, the rate and extent of diffusion and absorption by soil water, the absorption of the gas by soil particles, and its decomposition by certain soil constituents. In addition, the effect of soil fumigants on microorganisms such as protozoa and nitrifying bacteria must be determined.

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### *Use of Sprays*

The use of insecticides against subterranean insects has never been developed and presents many problems for investigation similar to those mentioned for soil fumigation. Alwood (1888) experimented with kerosene emulsion against the grubs of *Cotinis nitida* with some degree of success. Cotton (1918) and Davis (1920) tried insecticides on white grubs with no promising results.

Another phase of soil study in relation to the use of sprays is suggested by the papers of Headden (1908) and Ball (1909) on the arsenical poisoning of fruit trees. In the spraying of trees or other plants with arsenical or contact sprays, varying amounts of the material fall to the ground at the time, while practically all of it ultimately reaches the soil. In the case of orchards, where a number of applications are made annually, the amount of poison reaching the ground becomes large, and this raises the question of the effect of spray materials on the soil. Headden, after investigating a diseased condition of fruit trees in Colorado, attributed much of the trouble to arsenical poisoning. Ball, while not agreeing with many of Headden's conclusions, states that the entire subject of arsenical poisoning is a matter for careful and exhaustive investigation.

### *Use of Repellents*

The use of repellents for the prevention of injury to seeds between the time of planting and germination by such insects as ants, wireworms, false wireworms, and seed maggots is one of the older remedies advocated. The list of repelling agents recommended at various times is extensive, and it is necessary to mention only some of the more common ones, such as kerosene and other petroleum oils, crude carbolic acid, creosote, coal tar, turpentine, and oil of tansy. Three distinct methods of application are recognized: dipping or soaking the seed in a repelling agent; mixing the repellent with some fertilizer—for example, bone meal—and sowing with the seed; and the application of the repellent to the surface of the ground. The first method is generally advocated in the case of injury to germinating seed, the second has received attention in connection with the corn-root aphis, and the third has been recommended against the seed-corn maggot.

While the use of repellents has long been advocated, the conflicting results which have been obtained indicate that there is opportunity here for investigational work. A summary of the experimental work indicates that no satisfactory substance has been found which can be depended upon under the varying conditions existing in the soil. The problems connected with the use of repellents must be along two general lines: (1) the development of a repellent that is objectionable to the insect and at the same time not injurious to the seed, and (2) the influence of soil conditions on the effect of the repellent against the insect and on the germination of the seed.

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### *Miscellaneous Control Measures*

Various control measures are advocated from time to time which involve a knowledge of soil conditions and the effect which these measures will have on the ground. The use of such fertilizers as lime, kainit, and nitrate of soda is often recommended either as an insecticide or for the purpose of stimulating growth, thus enabling the plant to overcome insect injury. Under this category might be mentioned the dynamiting of the soil suggested by Cotton (1918) to destroy white grubs, the use of tile drains as recommended by Hyslop (1915) for the control of certain species of wireworms, and irrigation advocated by Parker (1915) against the sugar-beet root-louse.

## Summary and Conclusions

In conclusion, the writers desire to emphasize that this paper is a preliminary presentation of the relations of insects and soil, a complete discussion of which would fill a large volume. No attempt has been made to cover the entire field nor to make an exhaustive review of the literature. It has been the purpose rather to emphasize the importance of the soil as an environment. Much has been written on the biology of aquatic situations and plant associations, but the thin layer of soil which supports all plant and animal life is still open for extensive investigation. The problems are unlimited and are of the greatest fundamental importance to the progress of agriculture. To the entomologist the field is especially attractive. The soil is a complex of many factors which separately or conjunctively are of vital importance to insect life. Insects constitute one of the largest groups of the soil fauna, and practically all orders are represented. The principal uses which insects make of the soil are for shelter, protection, material of abode, food, moisture, air, heat, and as an avenue of travel. Insects exhibit many striking modifications and adaptations for living in the soil environment. The reciprocal benefits to the soil through insect activities are numerous and varied and may be classed as soil formation, renovation, and maintenance. The influence of the great number of interacting factors of the soil environment tax the resources of the investigators in this field. And finally the economic entomologist finds that a study of the soil is fundamental to the development of many control measures.

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# EFFECT OF REMOVAL OF THE VIRGIN WHITE PINE STAND UPON THE PHYSICAL FACTORS OF SITE

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It has long been a matter of speculation to what extent the complete or partial removal of the dense virgin timber alters the air and soil temperature in relation to humidity, soil moisture, and evaporation. Information on this subject would be of value in explaining the survival and growth of seedlings under different conditions, and might also be of use in a study of invasion or succession of vegetation after cutting and in fire protection. In order to secure such data, therefore, the U. S. Forest Service on July 12, 1919, installed three meteorological stations near the Priest River Forest Experiment Station in northern Idaho.

Since it was possible to keep the records at these stations for only a limited period, July and August, the months which are the hottest and most critical part of the growing season, were selected. Much credit is due Mr. Herman Bauman, Forest Service Field Assistant in 1919, for his conscientious care and painstaking accuracy in obtaining the records.

The stations were installed on the Binkly sale area, near the Priest River Forest Experiment Station. Station A was located on land cut clear in 1909–1910, about 250 feet south from the edge of the 300-year-old western white pine stand. On this site there are a few down logs and stumps, and practically no forest reproduction and no trees. Station B was placed about 400 feet north well within the tract logged in 1918, where there were several large western hemlocks and western red cedars, which are usually associated with white pine and made about one third forest cover. There was considerable unburned slash on the ground, but none right at the station. Station C was placed well within the uncut virgin timber, at least 300 feet from the opening on the south side.

Each station was equipped with maximum and minimum air thermometers of the Weather Bureau pattern, and Stations A and C had air thermographs and soil thermographs. These instruments were placed 4½ feet above the ground within a box made of half-inch board, painted white on the outside, and open to the north. At each station there was one psychrometer and one Livingston porous cup cylindrical atmometer. The latter was placed 6 inches above the ground; the bottle containing the water was placed entirely below the surface.

Daily soil temperature readings and semi-weekly soil moisture samples were obtained at a depth of 6 inches near each station on a bared plot of



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ground one meter square away from all roots. The records, except soil samples, were taken at 5 P.M. each day from July 12 to August 31.

A summary of the differences in air and soil temperature, relative humidity, evaporation, and soil moisture is given in the following table, and the averages of the daily thermograph records are shown in figure 1.

TABLE I. *Air temperature, relative humidity, evaporation, soil temperature and soil moisture averaged for each of three periods*

| | Air Temperature | | | Relative Humidity 5 P.M. | Average Daily Evaporation | Soil Temperature at 6″ | Soil Moisture at 6″* | Record |
|---|---|---|---|---|---|---|---|---|
| | Max. | Min. | Range | | | | | |
| | °F. | °F. | °F. | Percent | c.c. | °F. | Percent | |
| Station *A* in the open . | 90.9 | 40.1 | 50.8 | 21.5 | 33.6 | 64.0 | 31.6 | July 13 to 31 inc. |
| | 84.1 | 41.3 | 42.8 | 37.0 | 45.3 | 63.4 | 47.7 | August 1 to 15 inc. |
| | 88.1 | 37.0 | 51.1 | 33.5 | 27.0 | 62.1 | 36.9 | August 16 to 31 inc |
| Station *B*, ½ forest cover..... | 88.8 | 45.3 | 43.5 | 24.0 | 34.0 | 60.8 | 23.5 | July 13 to 31 inc. |
| | 81.6 | 45.4 | 36.2 | 39.4 | 21.0 | 59.5 | 28.4 | August 1 to 15 inc. |
| | 85.6 | 42.3 | 43.3 | 35.5 | 25.8 | 59.5 | 28.1 | August 16 to 31 inc. |
| Station *C*, full forest cover..... | 83.6 | 47.1 | 36.5 | 28.0 | 19.8 | 54.1 | 28.0 | July 13 to 31 inc. |
| | 76.3 | 47.2 | 29.1 | 45.5 | 11.7 | 55.0 | 31.4 | August 1 to 15 inc. |
| | 81.0 | 44.2 | 36.8 | 32.1 | 16.5 | 55.0 | 32.6 | August 16 to 31 inc. |

TABLE II. *Summary of records from July 13 to August 31*

| Stand Conditions | Air Temperature | | Relative Humidity 5 P.M. Per Cent. | Daily Evaporation c.c. | Soil Temperature at 6″ °F. | Soil Moisture at 6″ Per Cent. |
|---|---|---|---|---|---|---|
| | Av. Max. °F. | Av. Min. °F. | | | | |
| Open.... | 87.7 | 39.5 | 30.7 | 35.3 | 63.2 | 31.6 July<br>36.7 Aug. |
| ½ cover.. | 85.3 | 44.3 | 33.0 | 26.9 | 59.9 | 23.5 July<br>28.1 Aug. |
| Uncut... | 80.3 | 46.2 | 35.0 | 16.0 | 54.7 | 28.0 July<br>32.6 Aug. |

TABLE III. *Average of Air and Soil Thermograph Records for August, Degrees F.*

| Location | A.M. | | | | | Noon | P.M. | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 4 | 6 | 8 | 10 | 12 | 2 | 4 | 6 | 8 | 10 | 12 |
| Air Temperature in open | 42.7 | 40.4 | 39.5 | 50.4 | 64.5 | 76.7 | 82.4 | 83.3 | 78.5 | 61.2 | 51.0 | 46.1 |
| Air Temperature in forest | 50.7 | 47.9 | 46.0 | 47.6 | 57.7 | 67.4 | 47.1 | 76.1 | 73.6 | 65.9 | 56.6 | 53.9 |
| Soil Temperature in open | 64.5 | 64.1 | 63.3 | 62.6 | 61.8 | 61.4 | 61.6 | 62.1 | 63.1 | 63.9 | 64.2 | 64.4 |

The air in the uncut forest is about ten degrees warmer than in the open at night, and about ten degrees cooler during the hot part of the day. The curves cross at 7:30 A.M. and 7:30 P.M. for July and August (see fig. 1).

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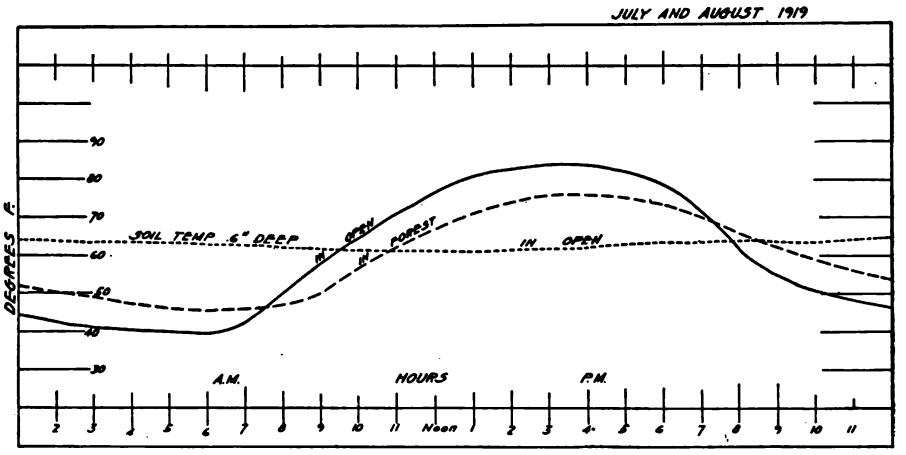


FIG. 1. Showing the influence of the forest in keeping the air temperature cooler in the daytime and warmer at night. Curves, solid and dash, are air temperature

Soil temperatures further show the influence of the forest cover. In the clear-cut area the soil temperature fluctuates 4 and 5 degrees F. between the maxima and minima. The soil thermograph record within the forest shows a variation of only one degree, and the maxima and minima occur from three to four hours later than in the open (see fig. 2).

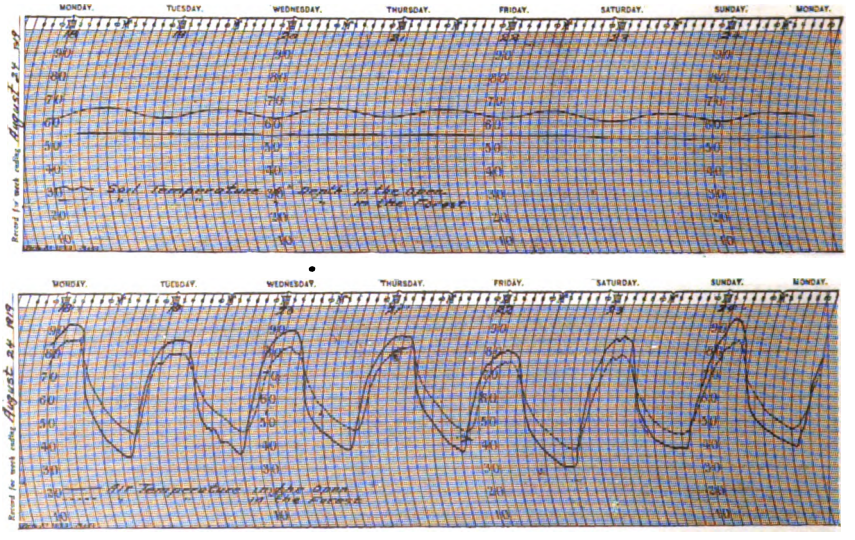


FIG. 2. Thermograph records of soil temperature at 6 inches, above; and of air temperature, below. Soil temperature shows fluctuations in the open, as compared with uniformity under the forest. Air temperature also shows less fluctuation in the forest, with lower maxima and higher minima.

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Another matter of interest is that the temperature of the soil in the open reaches the highest point between 12 and 2 o'clock at night, and the lowest point at 2 o'clock in the afternoon. The highest soil temperatures in the forest, on the other hand, occurred at about 4 o'clock in the morning.

Perhaps the difference in evaporation expresses better than any other datum the relative severity of the site. It is more than twice as great in the open as under timber, and on the partly cut area is very close to the average between that of the open and of the forest.

A lower soil moisture under the virgin timber than in the open may seem somewhat of a surprise; yet we must remember that these big trees have their greatest transpiration at this time of the year, and therefore demand much moisture from the soil. Also a considerable amount is intercepted by the crowns. The amount of moisture at any of the stations is not considered too little for white pine seedlings, and the survival of these seedlings on the cut-over area would depend more on whether or not the amount of sunshine or the air temperature were too great, or the rate of transpiration too rapid. In the absence of well-controlled tests on the influence of these factors upon the native coniferous seedlings it it not possible to state anything with finality. However, many of the one-year-old natural white pine seedlings died during the dry and warm months of 1919 on the area where only one third forest cover was maintained.

The complete opening of the site renders it almost totally unfavorable to natural establishment of hemlock and cedar, and somewhat precarious for white pine seedlings. Many of the evergreen plants which usually grow underneath and among the white pine stands, such as *Coptis trifoliata, Cornus canadensis, Pachystima myrsinites, Aralia nudicaulis,* and a great many more tender and moisture-loving plants, among which are *Circaea pacifica, Claytonia perfoliata, Galium borealis,* and *Montia spatulata,* disappear in the clearings. The habitat in the open is more suitable for *Rubus, Lonicera, Linnaea, Spiraea, Sambucus, Ceanothus,* and a great many grasses and sedges which are frequently found in the more open western yellow pine and Douglas fir stands. In the course of eight to ten years the grasses often become altogether too dense for natural reestablishment of the forest.

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# A QUANTITATIVE AND SEASONAL STUDY OF A PINE-DUNE ANIMAL COMMUNITY[1]

NELL JACKSON SANDERS AND VICTOR E. SHELFORD

## Introduction

Numerous studies of the quantity of life in water have been made; the quantity at different levels, at different hours of the day, etc., has been determined. Very little work of this character has been done on land. McAtee, Wolcott, and Beebe have covered grassland and forest floor, but we know of no attempt to estimate the entire animal population in a tree-covered area.

In addition to the quantitative problems a number of questions relative to the movements of animals arise. Do animals migrate back and forth from one plant community to another? When temperature and moisture conditions within a given plant community change radically, do animals shift from one zone or stratum to another? In other words, are there horizontal and vertical migrations? Or will animals found in the shrubs remain there throughout the day irrespective of changes of conditions? Animals free to shift back and forth are a much more sensitive index than plants.

## Locality and Methods

The observations here reported were made chiefly during the summer of 1914 in a pine hollow in the dune region at the south end of Lake Michigan (figs. 1, 2, 3). This hollow was situated between advancing dunes on the north and west, and an undrained reed and sedge marsh on the south, cut off from the Grand Calumet River by several large dunes. To the east lay an expanse of low dunes.

The chief tree of the station was Jack pine, *Pinus banksiana.* Other vegetation included willow, *Salix glaucophylla;* bearberry, *Arctostaphylos uva-ursi;* common juniper, *Juniperus communis;* poison sumach, *Rhus toxicodendron;* choke cherry, *Prunus Virginiana;* red-osier dogwood, *Cornus stolonifera;* horse mint, *Monarda punctata,* etc. The ground was partly open, the soil a light sandy loam. Near the margin the vegetation changed abruptly to sedges and swamp grasses which extended out into the open water of a shallow pond about two hundred feet in diameter. The work was confined entirely to a study of quantity and of the correlation of local, especially vertical, animal distribution with temperature and evaporation. Collections were made and temperature and evaporation recorded in each of the levels commonly recognized, viz., ground, herbs, shrubs, and trees, between July 1 and

[1] Contribution from the Zoological Laboratory of the University of Chicago and from the Zoological Laboratory of the University of Illinois.



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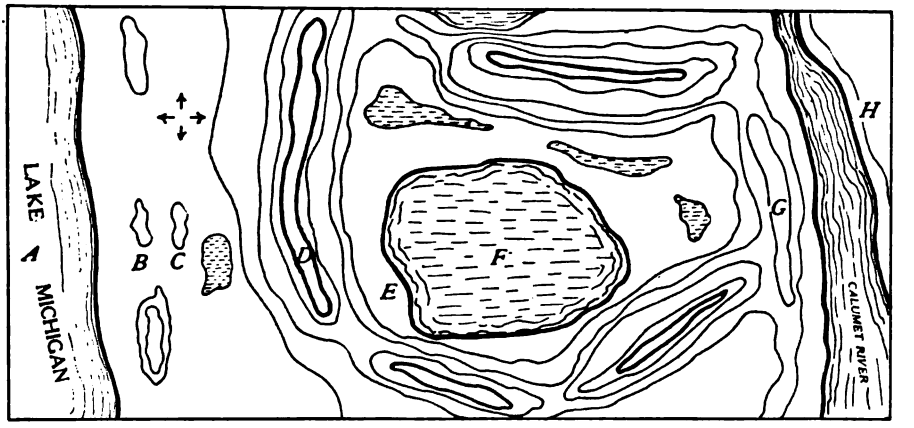


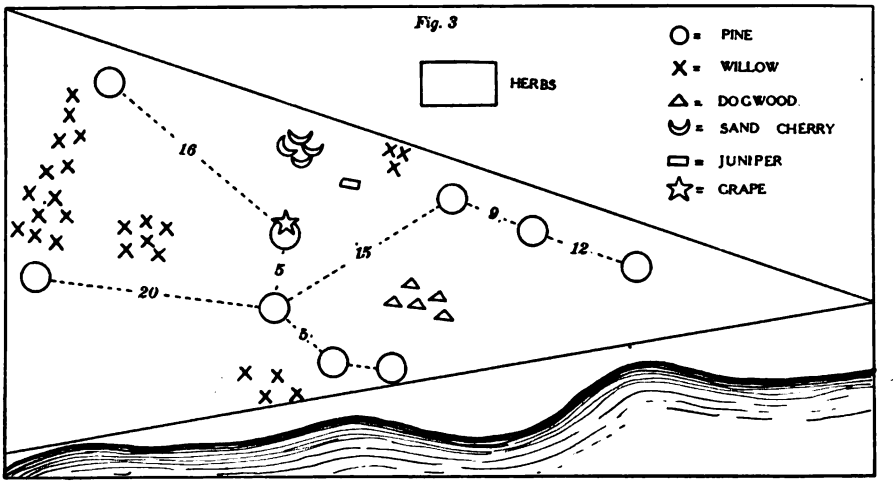


FIGS. 1, 2, and 3. 1. Cross section of the area studied.

2. Map of environs of the plot studied: *A*, Lake Michigan; *B*, sand cherry and sand-binding grass; *C*, cottonwood dunes; *D*, young cottonwood forest starting at lake level; *E*, pine hollow; *F*, swamp of sedges, rushes, and open water; between *G* and *H*, Grand Calumet River; *H*, oak woods on old dunes. Scales of figs. 1 and 2 about 200 feet to the inch.

3. Detailed map of the area of study. Numbers indicate distance in feet between trees and shrubs.

August 30. This was done regularly every four or five days from all the levels at about 8:30 A.M. In addition, during two full days, the observations and collections were made in the various levels at intervals of four hours

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between 4:30 A.M. and 8:30 P.M. All of the specimens collected during one of these days were sent to specialists for identification to discover whether upward or downward migration takes place as the temperature or evaporation rate changes during the day. Dr. Charles A. Hart and J. R. Malloch, of the State Entomologist's Office at Urbana, and Mr. Nathan Banks, of East Falls Church, Virginia, identified the specimens. Dr. C. P. Alexander kindly assisted with the lists. The specimens taken the other days were used for quantitative comparison only.

The ground collections were made where there were only scattered short-stemmed herbs. An actual count was made by forcing the open end of a bucket 25 cm. (10 in.) in diameter into the soil. By pouring a small quantity of a mixture of chloroform and gasoline through an opening in the inverted bottom, all the animals on the ground under the bucket were killed. It was difficult to see small insects such as aphids in the light soil. By using a fine sieve it was possible to obtain many which otherwise would have escaped observation. The other collections were obtained by making four strokes at each level with a close cotton net on a ring 30 cm. in diameter, with a handle 70 cm. long. To reduce the collections made with the bucket and net to the same value, sweeping with the net was followed in the same type of vegetation by bucket counting. It was found with a number of trials that *three* sweeps of the net yield essentially the same number of animals from the vegetation as one bucket counting. Three strokes with the net equal approximately .022 cubic meter of average denseness; four strokes equal .029 cubic meter.

## Space Inhabitable[2]

The plot was the approximate equivalent of a rectangle eleven meters (35 ft.) by fourteen meters (45 ft.), or an area of one hundred fifty-four square meters (1,575 sq. ft.).

### *a.* Herb Cover

Herbs covered two thirds of the area, and one third was bare. The average cover was forty-five cm. (18 in.) in height. The herb cover, if uniformly distributed over the area, was 30 cm. or one foot deep.

### *b.* Shrub Cover

A typical willow, with branches and leaves, is one meter (3 ft.) in diameter and 1.25 meters (4 ft.) tall. The general form approaches that of a sphere. The space occupied by each was .7 cu. m. (24.4 cu. ft.), and for twenty-six the space was 18.2 cu. m. (635.5 cu. ft).

A typical dogwood is an inverted cone, spreading 3.048 m. (10 ft.) at the top and 2.133 m. (7 ft.) high. The space occupied by each was 5.2 cu. m. (183.26 cu. ft.); for five it was 26 cu. m. (196.30 cu. ft.).

The four sandcherry shrubs were about equal to the willow, or .7 cu. m. (24.439 cu. ft.) $\times$ 4 equals 2.8 cu. m. (97.756 cu. ft.) total.

[2] Approximations only.

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The total space of shrubs was 47 cu. m. (1,649.57 cu. ft.); 47 cu. m. (1,649.57 cu. ft.) divided by 154 sq. m. (1,575 sq. ft.) equals approximately the average denseness to a depth of .31 meter (or 1 ft.).

### *c.* Pine Tree Cover

There were nine trees with crowns 4.6 m. (16 ft.) in diameter at the base and 8.5 m. (28 ft.) tall. The cone began 2.13 m. (7 ft. from the ground).

The space occupied by each tree cone was 46.7 cu. m. (1,649 cu. ft.). The total space of nine trees was 420.3 cu. m. (14,842 cu. ft.), which, divided by 154 sq. m., gives a depth of 2.8 m. (9.4 ft.).

## Animal Population

### *A.* For the Season

#### 1. *Subterranean Stratum*

The animals of the subterranean stratum were not studied as systematically as those above ground.

The chief species are tiger-beetles and their larvae, Digger wasps, ants, and occasional white grubs and ground-beetle larvae. They were estimated, on the basis of considerable digging, at 100,000 per acre or 250,000 per hectare.

#### 2. *Ground and Lowest Herbs*

The factor for converting the counts secured by the bucket to numbers of animals per hectare is 207,800, and per acre is 84,000. The counts were made where the vegetation was sparse, and none were taken under heavier cover. General experience shows that increase occurs as vegetation increases, hence the population on the ground generally may be expected to have exceeded the numbers estimated below.

List I. *Number of animals in the ground stratum with lowest herbs. (Collected from 490 sq. cm.)*

| Month | | | Total | Thousands of Individuals Per Hectare |
|---|---|---|---|---|
| July | 1 | 1 midge, 1 mosquito, 2 aphids | 4 | 830 |
| | 6 | 2 aphids | 2 | 415 |
| | 10 | 1 lepidopterous larva, 2 strawberry aphids, 1 insect egg | 4 | 830 |
| | 15 | 2 juvenile spiders, 11 aphids, 1 small fly | 14 | 2,909 |
| | 19 | 1 small spider, 1 small fly, 1 ant | 3 | 623 |
| | 24 | 4 aphids, 1 small spider, 2 lepidopterous larvae, 1 leafhopper | 8 | 1,662 |
| | 28 | 2 white scale insects, 9 aphids, 1 large ant, 1 small fly, 4 scales on strawberry petiole | 17 | 3,532 |
| Aug. | 1 | 17 strawberry aphids | 17 | 3,532 |
| | 5 | 3 ants, 6 aphids, 1 leafhopper | 10 | 2,078 |
| | 9 | 1 chrysomelid beetle, 3 aphids, 1 ant | 5 | 1,039 |
| | 13 | 1 ant, 1 leafhopper, 1 spider | 3 | 623 |
| | 18 | 6 strawberry aphids | 6 | 1,246 |

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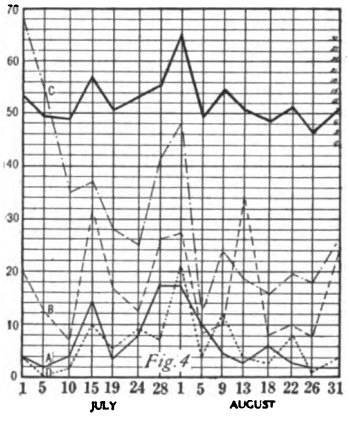
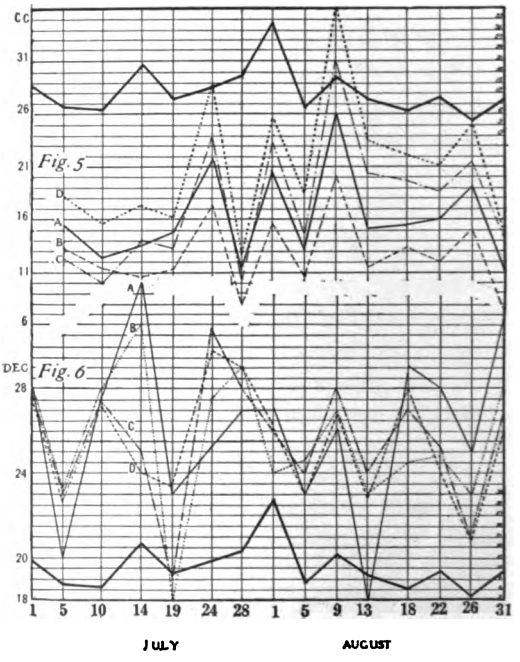
| | | | |
|---|---|---|---|
| 22 | 1 queen ant, 1 midge, 1 spider | 3 | 623 |
| 26 | 2 ants | 2 | 415 |
| 31 | 1 leafhopper, 1 ant | 2 | 415 |
| | Total | 100 | 20,772 |
| | Average | 6.6 | |
| | " Per Hectare | | 1,384 |
| | " Per Acre | | 560 |

### 3. *Population of the High Herb, Shrub, and Tree Strata*

The collections as given are 4 strokes of the sweep net, and are reduced to three strokes (the bucket equivalent) by multiplying by ¾.

*List 2. Herbs.*—The average height of the herbs on two thirds of the area is 45 cm. (18 in.), which would cover the total area 30 cm. high. The factor ($\frac{3}{4} \times \frac{2}{3} = \frac{1}{2}$) becomes $\frac{207,800}{2}$ or 103,900 for number per hectare (42,000 per acre).




FIGS. 4, 5, and 6. 4. Number of individuals taken at intervals of 4 or 5 days in the quantitative collections during July and August, 1914. *A*, from the ground (counted); B, from herbs; *C*, from shrubs; *D*, from trees; *B*, *C*, and *D*, with 4 sweeps of net. Heavy line shows total population in millions per hectare, with scale at right.

5. Evaporaton in c.c. per day, from readings at intervals of 4 or 5 days. *A*, on the ground; *B*, *C*, and *D*, at herb, shrub, and tree levels respectively. Heavy line same as in fig. 4.

6. Temperatures in degrees Centigrade, at same levels as in 5. Heavy line same as in 4.

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LISTS 2, 3 AND 4: *Numbers of animals in the high herb, shrub and tree strata.*

| Date | List 2. Herbs | | List 3. Shrubs | | List 4. Trees | |
|---|---|---|---|---|---|---|
| | No. Col. | Thousands per Hectare | No. Col. | Thousands per Hectare | No. Col. | Thousands per Hectare |
| July 1 | 21 | 2,182 | 68 | 7,065 | 4 | 3,900 |
| 6 | 12 | 1,247 | 57 | 5,922 | 1 | 975 |
| 10 | 7 | 727 | 35 | 3,636 | 2 | 1,950 |
| 15 | 31 | 3,221 | 37 | 3,844 | 10 | 9,750 |
| 19 | 17 | 1,766 | 28 | 2,909 | 5 | 4,875 |
| 24 | 13 | 1,350 | 25 | 2,597 | 9 | 8,775 |
| 28 | 26 | 2,701 | 41 | 4,260 | 7 | 6,825 |
| Aug. 1 | 27 | 2,805 | 48 | 4,987 | 21 | 20,775 |
| 5 | 9 | 935 | 12 | 1,247 | 4 | 3,900 |
| 9 | 10 | 1,039 | 24 | 2,494 | 12 | 11,775 |
| 13 | 34 | 3,532 | 19 | 1,974 | 4 | 3,800 |
| 18 | 8 | 831 | 16 | 1,662 | 3 | 2,925 |
| 22 | 10 | 1,039 | 19 | 1,974 | 8 | 7,600 |
| 26 | 8 | 831 | 18 | 1,870 | 1 | 975 |
| 31 | 23 | 2,389 | 26 | 2,701 | 5 | 4,875 |
| Total | 256 | 26,595 | 473 | 49,142 | 96 | 93,675 |
| Average | 17 | | 31.5 | | 6.6 | |
| Per H | | 1,773 | | 3,274 | | 6,245 |
| Per A | | 717 | | 1,324 | | 2,528 |

*List 3. Shrubs.*—The average height of the shrubs equals the average height of the herbs; the factors are the same.

*List 4. Trees.*—The tree crowns cover the ground to an average depth of 2.9 m. (9 ft.). The hectare factor is 975,000 (acre, 395,000).

### 4. *Total Population*

The total estimated population varied greatly from day to day, as the table below indicates.

LIST 5. *Population in thousands of individuals on different dates.* (*Subterranean population omitted*)

| July | Thousands per Hectare | Aug. | Thousands per Hectare |
|---|---|---|---|
| 1 | 13,977 | 1 | 32,081 |
| 6 | 8,559 | 5 | 8,160 |
| 10 | 7,148 | 9 | 16,347 |
| 15 | 19,724 | 13 | 9,929 |
| 19 | 10,173 | 18 | 6,664 |
| 24 | 14,384 | 22 | 11,236 |
| 28 | 17,318 | 26 | 4,091 |
| | | 31 | 10,380 |

The mean population according to the above estimate is upwards of 12,600,000 per hectare, or approximately 5,000,000 per acre. McAttee found 1,216,880 per acre of forest floor and 13,654,710 per acre of meadow. Our largest estimate is 13,073,000 per acre on Aug. 1; including the subterranean

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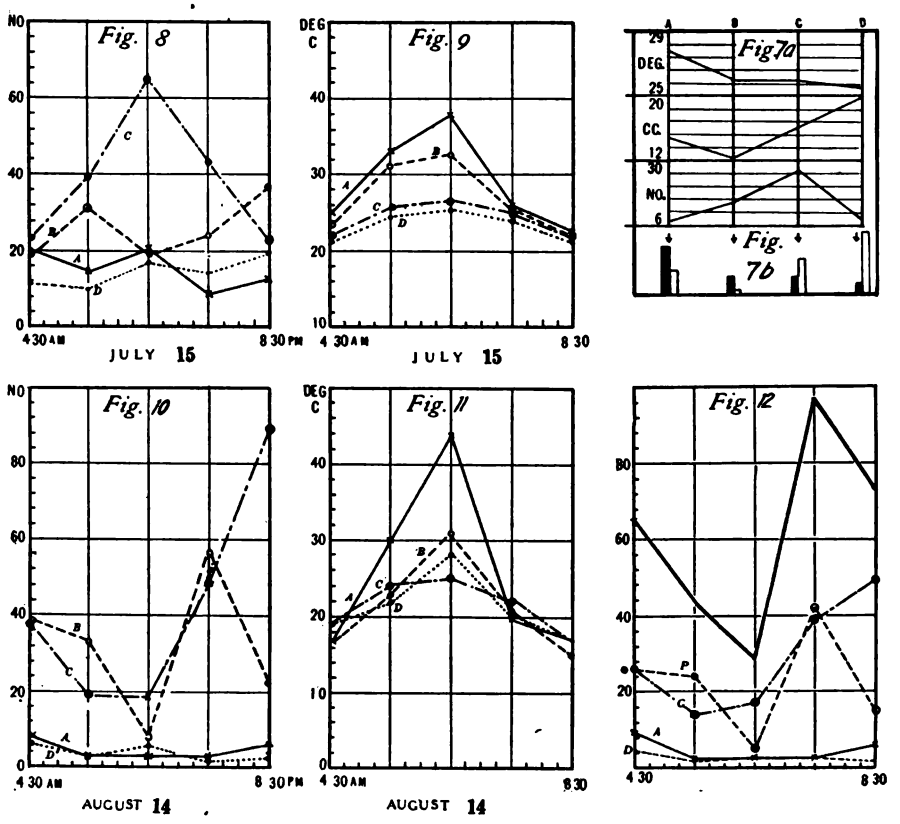
forms Wolcott found on meadow (vacant city lots in central Illinois), on an average, for spring months, 3,600,000 per acre. His tables indicate that about 600,000 subterranean animals should be deducted to make the figures comparable. List 5 and the graphs of general population in figure 4 show that the mean population rose through July, reaching a maximum August 1, and




FIGS. 7a, 7b, 8, 9, 10, 11, and 12. 7a. Graph showing *mean* temperatures, *mean* evaporation rate, and *mean* of actual number of individuals collected for July and August, 1914; *A*, ground; *B*, herbs; *C*, shrubs; *D*, trees.

7b. Graphic comparison of average temperature and evaporation rates at the four levels. Black columns are temperature, white evaporation.

8. Quantitative collections for July 15, 1914. *A*, from the ground, actual quantity; *B*, *C*, and *D*, from herbs, shrubs and trees respectively (4 sweeps of net).

9. Temperatures on July 15, 1914. *A*, at ground, *B*, at herb level (16 inches above ground), *C*, at shrub level (5 feet above ground); *D*, at tree level (16 feet above ground).

10. Quantitative collections for August 14, 1914. *A*, *B*, *C*, and *D* as in 8.

11. Temperatures on August 14, 1914, *A*, *B*, *C*, and *D* as in 9.

12. Same as fig. 10, with the omission of species known to breed in water. Double line shows total number.

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then falling off again through the month of August. With the exception of August 18, the collections were small when the temperature was low, and high when temperature was high. Roughly speaking, the same rise and fall is shown for temperature and evaporation.

## *B.* For Certain Days

### 1. *Qualitative and Quantitative Details of Two Days' Collecting*

Collections were made every four hours throughout the day on July 15 and August 14, beginning at 4:30 A.M. and continuing to 8:30 P.M. (omitting 12:30 A.M.). The following lists and figures, inclusive, give the results of these observations:

List 6. *Collections made every four hours on July 15 and August 14.*

| Stratum Group and Hour 8:30 a.m. | | Date: July 15 No. | Date: August 14 No. | Species Collected August 14 |
|---|---|---|---|---|
| Ground | Aphids (strawberry) | 14 | 9 | Aphididæ |
| | Flies | 3 | | |
| | Spiders | 3 | | |
| | Total | 20 | Total 9 | |
| Herbs | Ants | | 2 | *Lasius niger americanus* Emery |
| | Bugs | | 2 | *Balclutha impicta* V.D.<br>*Delphax* (sp) |
| | Flies | 7 | 4 | *Gonomyia sulphurella* O.S.<br>*Drosophila ampelophila* Loew.<br>*Sepsis cynipsea* Linn.<br>*Botanobia coxendix* Fitch |
| | Lacebug | 1 | 8 | *Corythuca marmorata* Uhl. |
| | Leafhoppers | 3 | 8 | *Empoasca mali* Le Baron<br>*Erythroneura vulnerata* Fitch<br>*Erythroneura comes vitis* Haec. |
| | Suiders | 3 | 3 | *Tetragnatha laboriosa* Htz.<br>*Clubiona abboti* Kock |
| | Total | 14 | Total 26 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 4 | 12 | *Culex* (sp.) |
| | Tree Frog | | 1 | *Hyla versicolor* Lec. |
| | Total | 4 | Total 13 | |
| | Total for the Stratum | 18 | 39 | |
| Shrubs | Bugs | 1 | 1 | *Lygus pratensis* Linn. |
| | Flies and midges | 10 | 4 | *Sapromyza tenuispina* Loew.<br>*Tanytarsus* sp.<br>*Sympycnus lineatus* Loew. |
| | Leafhoppers | 6 | 14 | *Empoasca mali* Le Baron<br>*E. obtusa* Walsh |

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| Stratum Group and Hour 12:30 p. m. | | Date July 15 No. | Date August 14 No. | Species Collected August 14 |
|---|---|---|---|---|
| | Spiders | 1 | 1 | *Epeiridae* |
| | | | 1 | *Philodromus ornatus* Bks. |
| | | | 5 | *Macrochiles* sp. and young |
| | Total | 18 | Total 26 | |
| | *Aquatic Breeders* | | | *Culex* sp. |
| | Mosquitoes | 4 | 5 | *Ceratopogon peregrinus* Joh. |
| | Flies and Midges | | 5 | *Chrysotus picticornis* Loew. |
| | | | 2 | |
| | Tree Frog | 1 | | |
| | Total | 5 | Total 12 | |
| | Total for the Stratum | 23 | 38 | |
| Trees | Beetles | | 2 | *Cryptocephalus schreibersi* Suffr. |
| | Spiders | 3 | 3 | *Theridium spirale* Em. |
| | Total | 3 | Total 5 | |
| | *Aquatic Breeders* | | | |
| | Midges | 1 | 1 | *Chironomus decorus* Joh. |
| | Mosquiaoes | 7 | | |
| | Total | 8 | Total 1 | |
| | Total for the Stratum | 11 | 6 | |
| Grand total for all strata | | | | |
| | Without aquatics | 53 | 65 | |
| | With aquatics | 72 | 92 | |
| Ground | Aphids | 11 | | |
| | Ants | | 1 | *Lasius niger americanus* Emery |
| | Flies | 1 | | |
| | Leafhoppers | | 1 | *Empoasca mali* Le B. |
| | Spiders | 2 | 1 | *Philodromus* sp. |
| | Total | 14 | Total 3 | |
| Herbs | Aphids | 8 | | |
| | Ants | 7 | 3 | *Lasius niger americanus* Emery |
| | Flies, etc. | 14 | 17 | *Drosophila adusta* Loew.; *Leptocera fontinalis* Fall. |
| | Leafhoppers | 1 | 4 | *Cicadula 6-notata* Fall.; *Empoasca mali* Le Baron; *Empoasca obtusa* Walsh; *Gypona 8-lineata* Say |
| | Spiders | 1 | | |
| | Total | 31 | 24 | |
| | *Aquatic Breeders* | | | |
| | Fly | | 4 | *Tanytarsus* sp. |
| | Midge | | 6 | *Ceratopogon fusculus* Coq. |
| | | | 10 | |
| | Total for Stratum | 31 | 34 | |

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| Stratum Group and Hour 4:30 p. m. | | Date July 15 No. | Date August 14 No. | Species Collected August 14 |
|---|---|---|---|---|
| Shrubs | Flies, etc. | 24 | 6 | *Chrysotus picticornis* Loew.<br>*Drosophila ampelophila* Loew.<br>*Gonomyia sulphurella* O.S. |
| | Leafhoppers | 10 | 7 | *Cicadula 6-notata* Fall.<br>*Empoasca mali* Le Baron<br>*Empoasca obtusa* Walsh<br>*Gypona 8-lineata* Say |
| | Caterpillar | | 1 | unidentified |
| | Spiders | 3 | 1 | *Tetragnatha laboriosa* Htz. |
| | Total | 37 | Total 14 | |
| | *Aquatic Breeders* | | | |
| | Midges | 0 | 2 | *Ceratopogon peregrinus* Joh.<br>*Chironomus festivus* Say |
| | Mosquitoes | 0 | 2 | *Culex* sp. |
| | Caddice Fly | 0 | 1 | |
| | | 0 | 5 | |
| | Total for Stratum | 37 | 19 | |
| Trees | Beetles | | 2 | *Cryptocephalus schreibersi* Suffr.<br>*Dicerca punctulata* Schön. |
| | Flies | 7 | | |
| | Spiders | 3 | | |
| | Total for Stratum | 10 | 2 | |
| Total for all Strata | | | | |
| Without aquatics | | 92 | 43 | |
| With aquatics | | 92 | 58 | |
| Ground | Ants | 1 | | |
| | Aphides | 17 | | |
| | Beetles | 1 | | |
| | Cricket | | 1 | *Ellipes minutus* Scudd. |
| | Flies | 1 | | |
| | Spiders | | 2 | *Dendryphantes octavus* Hentz |
| | Total | 20 | Total 3 | |
| Herbs | Ants | 3 | 1 | *Lasius niger americanus* Emery |
| | Flies, etc. | 8 | 2 | *Chrysotus picticornis* Loew. |
| | Leafhoppers | 1 | 2 | *Cicadula 6-notata* Fall.<br>*Empoasca mali* Le Baron |
| | Moth and larva | 2 | | |
| | Spiders | 4 | | |
| | Total | 18 | Total 5 | |
| Shrubs | Beetle | 1 | | |
| | Flies and midges, etc. | 38 | 8 | *Drosophila ampelophila* Loew.<br>*Gonomyia sulphurella* O.S. |

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| Stratum Group and Hour 8:30 p. m. | | Date July 15 No. | Date August 14 No. | Species Collected August 14 |
|---|---|---|---|---|
| | Damsel fly | 1 | | |
| | Leafhoppers | 4 | 5 | *Empoasca obtusa* Walsh<br>*Gypona 8-lineata* Say |
| | Moths and larva | 2 | | |
| | Spiders | 5 | 3 | *Dendryphantes octavus* Hentz<br>*Maevia vittata* Hentz-*niger* Hentz<br>*Thiodina* sp. |
| | Total | 51 | Total 17 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 14 | 2 | *Culex* sp. |
| | Total for the Stratum | 65 | 19 | |
| Trees | Flies and midges | 9 | | |
| | Lacebug | 1 | | |
| | Moth | 2 | | |
| | Spiders | | 3 | *Epeira* (very young) |
| | Total | 5 | Total 3 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 5 | 0 | |
| | Midges | 0 | 1 | *Chironomus fulvus* Joh. |
| | Total | 5 | Total 1 | |
| | Total for the Stratum | 17 | 4 | |
| | Grand Total All Strata Without aquatics | 102 | 28 | |
| | With aquatics | 121 | 31 | |
| Ground | Aphids | 4 | | |
| | Ants | 2 | | |
| | Beetles | | 1 | *Stenolophus ochropezus* Say |
| | Bugs | | 2 | Jassidae |
| | Spiders | 2 | | |
| | Total | 8 | Total 3 | |
| Herbs | Ants | 7 | 3 | *Lasius* sp. |
| | Bugs | 3 | 6 | Jassidae<br>*Erythroneura tricincta* Fitch<br>*Corythuca marmorata* Uhl.<br>*Dikraneura abnormis* Walsh |
| | Flies, etc. | 10 | 42 | *Drosophila ampelophila* Loew.<br>*Drosophila adusta* Loew.<br>*Drosophila amoena* Loew.<br>*Drosophila obesa* Loew.<br>*Leptocera fontinalis* Fall.<br>*Schoenomyza* sp.<br>*Sepsis cynipsea* Linn. |

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| Stratum Group and Hour 8:30 p. m. | | Date July 15 No. | Date August 14 No. | Species Collected August 14 |
|---|---|---|---|---|
| | Mosquitoes | 2 | | |
| | Spiders | 2 | 2 | *Philodromus*, young |
| | Total | 22 | Total 42 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 2 | 2 | *Culex* sp. |
| | Midges | 0 | 4 | *Chironomus* sp.<br>*Ceratopogon fusculus* Coq. |
| | Flies | 0 | 7 | *Tanypus monilis* Linn.<br>*Sympycnus lineatus* Loew. |
| | | 2 | 13 | |
| | Total for the Stratum | 24 | 55 | |
| Shrubs | Ants | | 4 | *Lasius niger americanus* Emery |
| | Bugs | 4 | 14 | *Empoasca mali* Le Baron<br>*Gypona 8-lineata* Say |
| | Flies, etc. | 37 | 24 | *Aphiochaeta* sp.<br>*Discocerina* sp.<br>*Drosophila obesa* Loew.<br>*Gonomyia sulphurella* O.-S.<br>*Leptocera fontinalis* Fall. |
| | Spiders | | 4 | *Philodromus ornatus* Banks young |
| | Total | 41 | Total 39 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 3 | 3 | *Culex* sp. |
| | Midges | 0 | 7 | *Chironomus* (*modestus*)<br>*Ceratopogon fusculus* Coq.<br>*Chironomus fulvus* Joh. |
| | | 3 | 10 | |
| | Total for the Stratum | 44 | 49 | |
| Trees | Beetles | | 1 | *Diabrotica 12-punctata* Fabr. |
| | Flies | 8 | | |
| | Spiders | 4 | 2 | *Epeira* sp.<br>*Theridium spirale* Em. |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 6 | | |
| | Total for the Stratum | 14 | 3 | |
| | Grand total for All Strata | | | |
| | Without aquatics | 83 | 87 | |
| | With aquatics | 94 | 110 | |

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| Stratum Group and Hour 8:30 p. m. | | Date July 15 No. | Date August 14 No. | Species Collected August 14 |
|---|---|---|---|---|
| Ground | Aphids | 11 | | |
| | Beetles and larva | 2 | 2 | *Cardiophorus*, larva |
| | Flies | | 4 | *Leptocera fontinalis* Fall. |
| | Total | 13 | Total 6 | |
| Herbs | Beetle (Chrysomelid) | 1 | | |
| | Flies, etc. | 35 | 12 | *Drosophila obesa* Loew. |
| | Leafhoppers | 1 | 2 | *Erythroneura comes vitis* Harris<br>*Erythroneura vulnerata* Fitch |
| | Spiders | | 1 | |
| | Total | 37 | Total 15 | *Theridium spirale* Emerton |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | | 8 | *Culex* sp. |
| | Total for the Stratum | 37 | 23 | |
| Shrubs | Beetle (Chrysomelid | 7 | | |
| | Flies, etc. | 13 | 26 | *Bezzia setulosa* Loew.<br>*Drosophila amoena* Loew.<br>*Drosophila obesa* Loew. |
| | Leafhoppers | 3 | 24 | *Erythroneura comes vitis* Harris |
| | Total | 23 | Total 49 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 2 | 39 | *Culex* sp. |
| | Total for the Stratum | 25 | Total 89 | |
| Trees | Ants | 3 | | |
| | Flies, etc. | 3 | 1 | *Drosophila obesa* Loew |
| | Leafhoppers | | 1 | *Erythroneura comes vitis* Harris |
| | Spiders (Young) | 9 | | |
| | Total | 15 | 2 | |
| | *Aquatic Breeders* | | | |
| | Mosquitoes | 4 | 2 | *Culex* sp. |
| | Total for the Stratum | 19 | 4 | |
| | Total all Strata | | | |
| | Without aquatics | 88 | 73 | |
| | With aquatics | 94 | 122 | |

## Migration

A study of the lists and of figures 7 to 11 show that a migration of aquatic species into the land habitats occurred at different hours on the two dates when collections were made. On July 15 the total at noon was increased by the influx of mosquitoes, while on August 14 the total at 8:30 P.M. was increased by the influx of aquatic breeders from other habitats. However, even the complete listing and identification of August 14 does not show consistent totals. It appears that animals are in an easier position to be captured

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under certain conditions than under others. These conditions fall at different times of day due to weather, etc. For example, at the time of the morning collection of August 14 the vegetation was wet in consequence of a heavy shower the day before. This moisture partially equalized the humidity and rate of evaporation at the different levels. The results are different from those obtained July 15.

The most convincing evidence of migration of animals from one level to another as conditions change is that obtained from observation of species. The table for August 14 gives much interesting data. The following cases of apparent migration are found:

Among the spiders, *Tetragnatha laboriosa* was in the herbs 4:30 A.M., and shrubs 8:30 A.M.; *Theridium spirale,* in the trees 4:30 P.M., and herbs 8:30 P.M.

For the insects, apparent migrations shrubwise during the day are *Botanobia coxendix, Culex* sp., *Erythroneura comes vitis, Drosophila ampelophila,* herbs to shrubs; *Chironomus fulvus,* trees to shrubs; *Lasius niger americanus,* ground and herbs to herbs and shrubs; *Drosophila amoena,* herbs to shrubs.

Evidences of migrations late in the day downward to lower levels are *Drosophila ampelophila,* shrubs to herbs, and *Leptocera fontinalis,* shrubs to ground.

In quantity as well as quality the movement seems to be shrubwise during the early day and downward at night. The shrubs show not only the greater number of individuals, but also the greater number of species.

The total number of different species at various levels are as follows:

Ground..... 10 species, average temperature 25.4°, range 25°
Herbs..... 34 species, average temperature 21.2°, range 16°
Shrubs..... 38 species, average temperature 21.0°, range 8°
Trees..... 11 species, average temperature 21.2°, range 11°

In terms of temperature, these results are not a coincidence; the greater number of species is to be found at the level where changes in temperature are least and, possibly, also where the temperature itself is medium compared to the other levels.

Horizontal migrations may account for the fluctuations of numbers of individuals of given species. Of the leaf hoppers, *Erythroneura comes vitis* was taken as follows August 14: At 4:30 A.M., 1 specimen; at 8:30 A.M., at 12:30 P.M., and at 4:30 P.M., no specimen; and at 8:30 P.M., 27 specimens. No doubt an inwards migration of this insect occurred toward nightfall. The influx of aquatic animals suggests the importance of checking against horizontal migrations in quantitative study.

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## Discussion and Summary

The following indicate the difficulties and matters to be taken into account in quantitative work:

1. The animal population rose during July, reached a maximum about August 1, and then declined.

2. The number of animals varied in a general way directly with temperature and evaporation.

3. The number of animals in the area studied was increased by influx from adjacent habitats, especially by water-breeding species from the near-by swamp.

4. Some animals migrate upward during the first half of the day and downward during the later portion.

5. The number of species and individuals is greatest in the shrubs.

6. The accessibility of animals varies with conditions and makes collections with nets, etc., variable.

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# THE SPHAGNUM BOGS OF MAZAMA DOME

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This paper deals with some small sphagnum bogs occurring at relatively high elevations and characterized by a very simple plant association.

Mazama Dome is a flat-topped mountain having an elevation of 6,000 feet (U. S. G. S., 1915). It is situated in Whatcom County, Washington, on a

Fig. 1. Bog bordering the lake on Mazoma Dome

spur extending westward from the main ridge of the Cascades to Mount Baker. Austin Pass crosses this spur between Mount Baker and Mount Shuksan at an elevation of 4,630 feet (U. S. G. S., 1915). Mazama Dome is between the pass and Mount Baker. The visits to the dome were made on August 6 and 7, 1921; August 5 and 8 were spent in observation of the sphagnum occurring in other places in the vicinity of the pass.



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At the time of these visits there was considerable snow on the summit of this dome, and, although the cairn of rocks marking the highest point was bare, a snow field began only a few yards from it. The bogs are on a bench-like flat, situated just to the south of and below the ridge occupied by this snow field, and receiving water in small rivulets from the melting snow. At the south side is an abrupt descent of several hundred feet. During the day-time in summer this flat has an abundance of light and moisture and the temperature of the air is rather high.

One bog, typical of this flat, forms the south side of a pond, on the north of which is a mass of loose rock. The pond seems to have originated from the obstruction of drainage on a very gentle slope by the growth of vegetation and the accumulation of the debris, either intact or partially decayed, resulting from this growth. The vegetation has thus formed a ridge or dam several feet high and only a foot or two wide at the top. The bog association occupies the top and the south side of this ridge.

The surface of this ridge of vegetation is at present composed almost entirely of living sphagnum. In this the most abundant plant is the swamp laurel, *Kalmia polifolia,* which was rarely found in the vicinity outside of sphagnum-dominated areas, while such areas were rarely found without this plant. All the Kalmia seen was small (usually 6 to 9 inches tall), and seems to be identical with the variety *microphylla.* It was in full bloom at the time of the visits.

The low bush huckleberry, *Vaccinium deliciosum,* was fairly abundant in most of this bog and was common in the vicinity. In a few places, mostly in the margin of the sphagnum-dominated area, the red heather, *Phyllodoce empetriformis,* grew with the three plants mentioned. This heather was very abundant in the vicinity, but practically stopped at the margin of the sphagnum. Partridge-foot, *Lutkea pectinata,* was also abundant in the vicinity, but very few specimens of it grew in the sphagnum.

A sedge, *Carex* sp., was abundant in the sphagnum next to the water of the pond, and formed much of the water margin of the ridge. Mosses, mostly *Hypnum* sp., other than sphagnum grew with the sedge at the margin of the water, often extending over the edge into the water. Sphagnum was not growing into the water of this pond at all.

Several samples of the substratum of this ridge were taken at a depth of 6 inches. Those under pure living sphagnum consisted of the same plant slightly decayed. Those under the tension line between sphagnum and the sedge were much more fibrous, but contained a little sphagnum.

This bog association is thus seen to be composed essentially of only two plants, sphagnum and swamp laurel, with a third (low-bush huckleberry) sometimes present; while other plants such as red heather and partridge-foot thrive in the vicinity, but are unable to enter the bog association to any considerable extent. This is a very simple bog association as compared with

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that found in other bogs of the Puget Sound region. Several of these, mainly at low levels, have been described by the writer (1913, 1919). In most of this region the bog association consists rather constantly of *Sphagnum* spp., Labrador tea, *Ledum groenlandicum;* swamp laurel, *Kalmia polifolia;* cranberry, *Oxycoccus oxycoccus,* and sundew, *Drosera rotundifolia,* with the occasional addition of other plants such as sweet gale, *Myrica gale;* a gentian, *Gentiana sceptrum,* and crowberry, *Empetrum nigrum.*

Vegetation seems to be advancing on the water of this pond. The sedge and mosses other than sphagnum are clearly the pioneers, the mosses being usually a little in advance of the sedge. Sphagnum itself is not functioning as a pioneer in the advance of the bog, nor is the bog association as such advancing directly on the pond. It advances only by the aid of the sedge-moss association. The samples of the substratum seem to indicate that the bog association has been dominant here for some time, and that, with the sedge-moss association functioning as the pioneer, it has been responsible for the building up of at least the upper portion of this ridge.

In other places in the vicinity there are similar ponds apparently formed in a similar way. They are on places where the substratum slopes gently to the south, and the south side of each is composed of a ridge of vegetation topped at present by the bog association, with the sedge-moss association next to the water and functioning as the pioneer. In only one case was sphagnum found growing directly into the water; here it extended out about a foot and occupied about 3 feet of the shore line. In a few places this simplified bog association, consisting mainly of sphagnum and *Kalmia,* was found on the flat in wet spots not bordering on ponds; in fact, most of these spots were not on water at all, although one was along a rivulet flowing down a slope of perhaps 15° or 20°. In this case there was the usual margin of sedge and mosses along the water.

The fact that the flora of these bogs consisted mainly of only a single species besides sphagnum does not seem to constitute a valid objection to calling them bogs or to calling their characteristic flora a bog association. It is simple as compared with that of many other bogs, but is none the less a bog association.

Sphagnum was common in the vicinity of Austin Pass at elevations mostly approximating 4,000 feet or more. Patches of this moss, mostly only a few feet in diameter, were found in small undrained places along the trail for a distance of 2 miles or so north of the pass, and for a like distance to the south. There was a good deal of snow in the vicinity of the pass at the time of the visits and it is possible that some sphagnum was covered which might be exposed in more favorable seasons.

No case was seen in which the sphagnum had exercised any selective influence on the plants growing in it. The flora of the patches of this moss was the same as that of the other undrained places in the vicinity, many of

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which had other mosses growing in them instead of sphagnum. A horsetail, *Equisetum* sp.; a sedge, *Carex* sp., and green hellebore, *Veratrum viride,* were common in such places. Such patches of sphagnum are rather numerous in both the Cascades (Rigg, 1919) and the Olympics.

It is possible that these patches of sphagnum may represent early stages in bog succession in which the products of decay are not yet sufficient in quantity to exercise a selective influence on the flora. However, the drainage from such places is merely slow; not obstructed to any considerable extent. If a bog developed, its surface would have to rise considerably above the surrounding area. No swamp laurel has been seen by the writer in the immediate vicinity of these sphagnum patches in either the Cascades or the Olympics.

On the basis of this lack of distinctive flora these sphagnum areas seem to be clearly distinguished from the sphagnum areas on Mazama Dome, which do have a distinctive flora which is practically always found in them and only rarely outside of them. It seems justifiable to use the term "bogs" for the latter, while not using it for the former. The writer has elsewhere (1916) proposed as a definition of sphagnum bog "that stage in the physiographic succession of an area during which its surface is entirely devoid of ordinary 'hard' soil, and is composed completely of living sphagnum moss under which is fibrous brown peat composed mainly or entirely of partially decayed sphagnum." It is now proposed to add to this definition the limitation that the bog exercises a distinctly selective influence on its flora.

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# THE ECOLOGICAL RELATIONSHIPS OF THE DRAGONFLIES OF THE BASS ISLANDS OF LAKE ERIE[1]

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The dragonfly fauna of the Put-in-Bay region is one of the most meager the writer has seen, but its very lacks and limitations make it one of the most interesting. The ecological groupings are so sharply defined that their relationships are outstanding. This obvious grouping of the species in the field leads us directly to a parallel division of the discussion as follows: (1) The lake species and their origin. (2) The pond species, their origin, and their succession as the ponds age. (3) The constant pressure of the pond species into the habitat of the lake species.

The data cover the time from June 20 to August 1, 1921, the opening and closing dates of the Lake Laboratory.

## 1. THE LAKE SPECIES AND THEIR ORIGIN

The biological station of Ohio State University is located at Put-in-Bay on South Bass Island, which is approximately five miles from the southern shore of Lake Erie. South Bass is the southernmost of the group of Bass Islands, which, with Kelly's, Pelee, and numerous smaller islands, stretch as an archipelago north to the Canadian shore (see the map, fig. 1). All are low limestone tables whose highest contours seldom rise more than ten feet above the lake surface. The island shores, except for a few bays with sand or gravel beaches, are perpendicular limestone cliffs about whose bases the waves beat continuously among the ledges and boulders (see fig. 2). The water in this western end of Lake Erie is only thirty feet deep; in fact, Lake Erie is the shallowest of the Great Lakes. Soundings show that the greater extent of this shallow bottom is covered with clay and sand. The strictly lake environment then, while great in extent, is extremely monotonous for a diversified Odonate fauna. It is, in fact, a very simple but very special environment consisting of the rocky shore line and flat lake bottom. As even thirty feet of water is too deep for Odonate larvae, this great area of bottom is excluded as dragonfly environment, leaving the rocky, wave-torn cliffs and boulder shores with their occasional sand or pebble beaches as the only freehold for these insects. Because of the many miles of such rocky shores the lake Odonata are still very numerous, but are reduced to the very few species that can survive among wave-washed rocks or perhaps that can emerge into adult life successfully on such shores.

[1] Contribution from the Department of Zoology and Entomology, Ohio State University, number 69.



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Along these rocky shores only four species of dragonflies are abundant. These are the little gray *Argia moesta,* the large *Gomphus plagiatus* and *Neurocordulia yamaskinensis,* and the great black and yellow *Macroma illinoiensis.* *Argia moesta* occurs in great numbers on all islands high enough

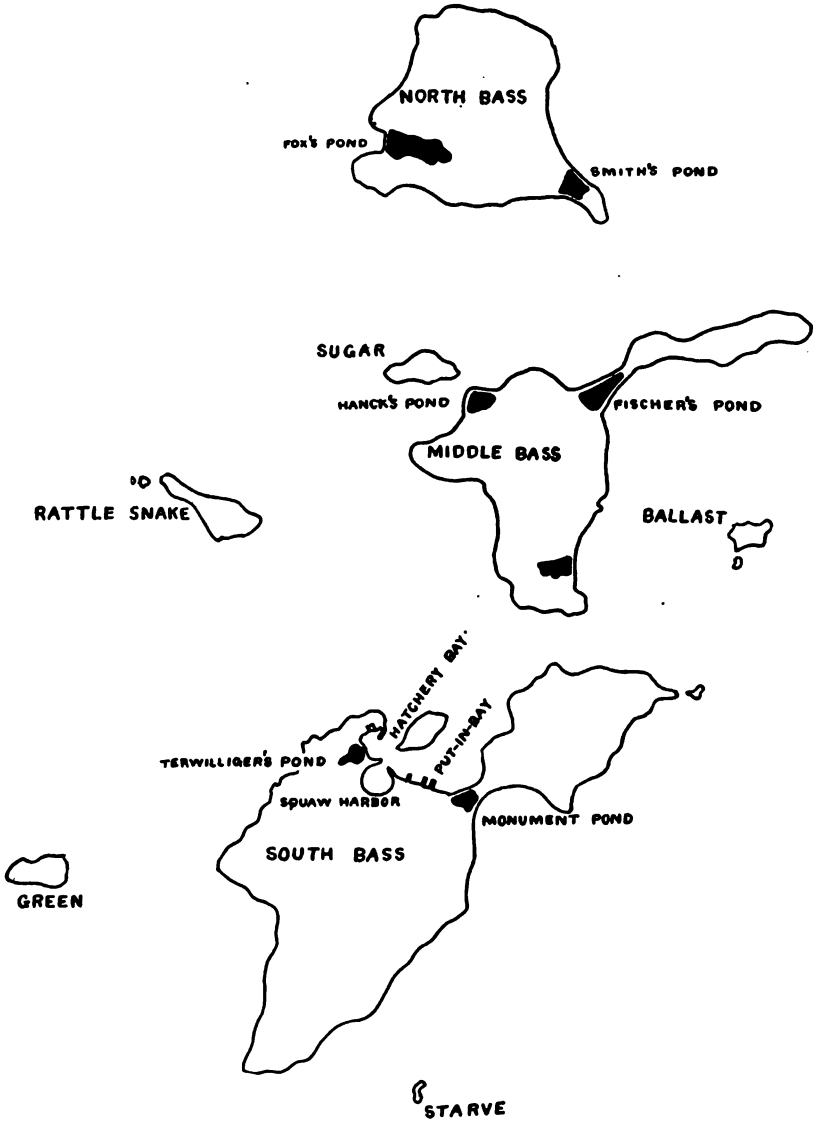


FIG. 1. Map of the Bass Islands of Lake Erie, showing the ponds and harbors.

to have a cliffy shore. It occurs in numbers also on East Sister, where the entire shore line is of coarse gravel. The other three occur in less numbers, yet are abundant. *Neurocordulia yamaskinensis* is crepuscular in

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habit, flying only at sunrise or sunset, or occasionally on cloudy days. It feeds on the great swarms of aquatic insects that come out of the lake each evening, while it spends its daylight hours sleeping in the trees. The other species are diurnal and roam the fields and woods for a more general diet.

Along the sand and pebble beaches occur *Gomphus vastus* and *Gomphus fraternus,* which are typical lake species (see fig. 3). Though very much restricted in its breeding sites because of the very few beaches, *Gomphus vastus* in season is the most abundant of the large dragonflys. *Gomphus fraternus* is seldom seen or caught.

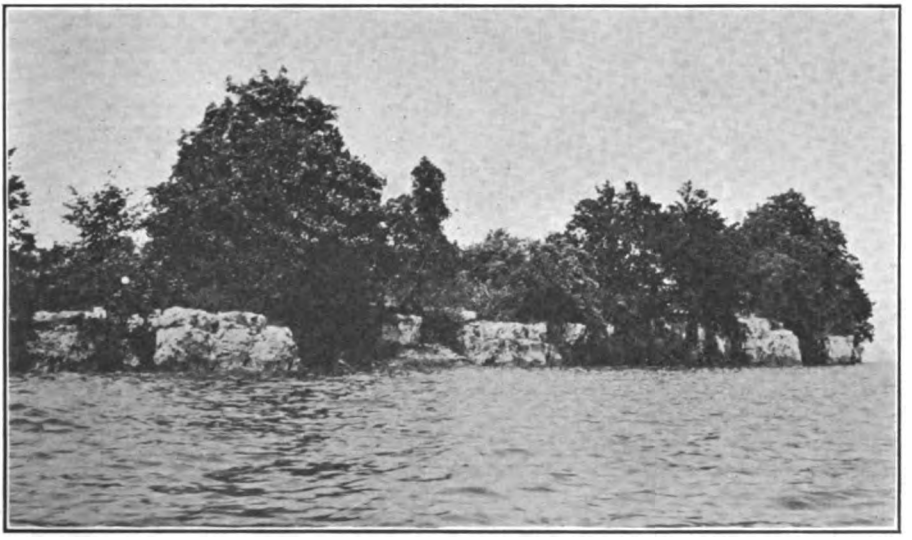

FIG. 2. The vertical limestone shore of Rattle-Snake Island. Habitat of *Gomphus plagiatus, Neurocordulia, Macromia* and *Argia*

The nymphs of the three lake species of *Gomphus* burrow in the mud and sand of the lake bottom. Why *plagiatus* should prefer such bottom near a rock shore, and the other two a bottom bordered by a beach, is not known. The nymphs of the other lake species are long-legged and scramble for a living among the rocks.

The origin of the lake species is similar to that of the other lake-shore inhabiting aquatic insects. These lake species have probably originated from the streams of the surrounding mainland. *Neurocordulia* probably comes from the streams of southern Canada, and *Argia,* the three *Gomphus,* and *Macromia* come from the streams of the Northern States. All the strictly lake species adapted to the well aerated and tempestuous waters of the shore are then true stream species. The three *Gomphus* larvae avoid the rough waters by their burrowing habits; the other three species have very vigorous long-legged larvae with strength enough to take care of themselves in spite of the waves.

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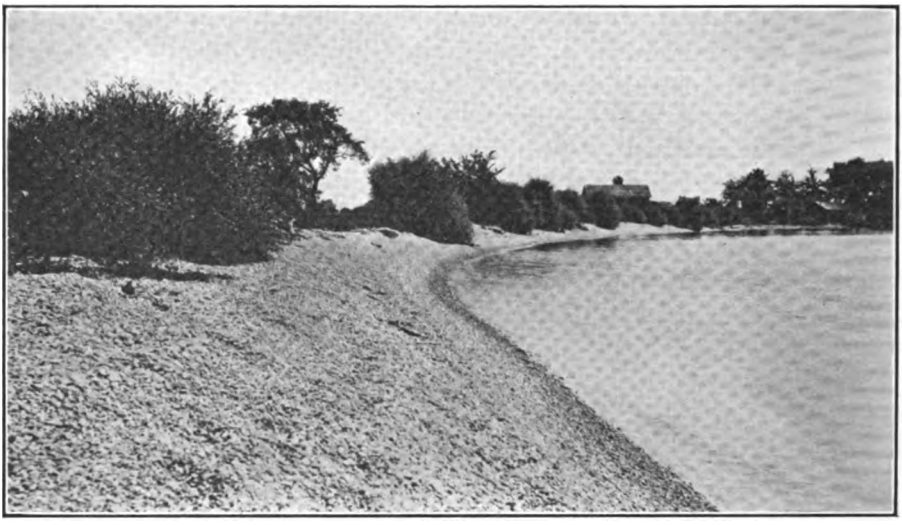

FIG. 3. Gravel bar closing Hanck's Pond on Middle Bass Island. Habitat of *Gomphus fraternus* and *Gomphus vastus*

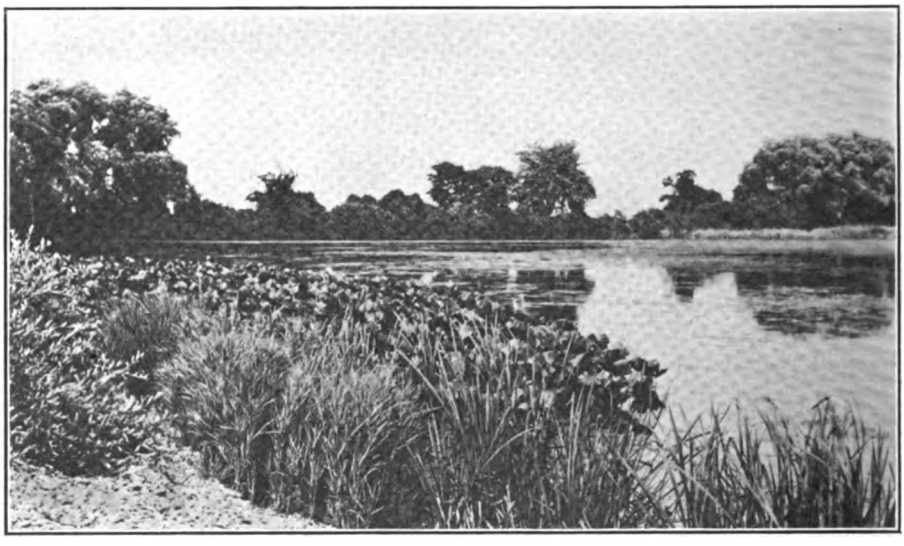

FIG. 4. Hanck's Pond, Middle Bass Island. This pond is at the peak of its development, supporting the full list of pond dragonflies

## 2. THE POND SPECIES, THEIR ORIGIN, AND THEIR SUCCESSION AS THE PONDS AGE

A further description of the islands is desirable to correctly place this series of species. The islands in their primitive condition were covered with

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hardwood forests that had cedar groves about their edges where the soil was shallow. Seven ponds occur on the three main islands: two on South Bass, three on Middle Bass, and two on North Bass. (Pelee and Kelley's Islands were not explored in this study.) These ponds are peculiar in their origin and development. All seem to have originated as small bays, which later have been cut off from their lake connection by gravel bars shoved up by wave and ice action.[1] They seem to have originated contemporaneously after the retreat of the ice, but some have aged more rapidly than others, so that a graduated series can be easily traced from the clean and open Put-in-Bay to the ecological climax of a grassy meadow or a hardwood forest protected from the lake by a gravel dyke, as exemplified in Fox's pond at Manilla Bay on North Bass (see figs. 5 and 6).

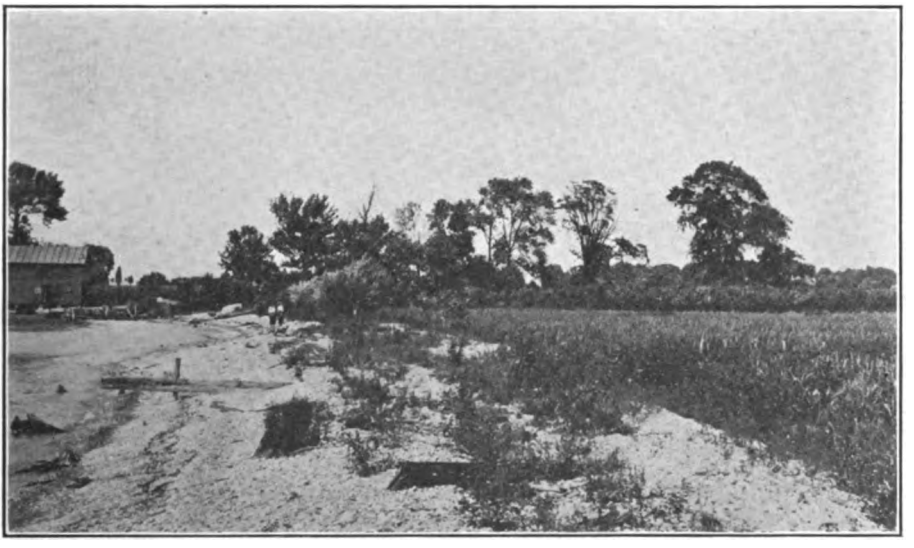

FIG. 5. Fox's Pond, North Bass Island. This is a pond in its old age, after it has become a Sparganium and sedge marsh, with the *Sympetrum* and *Lestes* dominant.

More specifically their development can be shown in the following series:

1. Put-in-Bay, South Bass. Open to the lake, deep, bottom of mud and sand, shores rocky or gravelly. Vegetation limited to diatoms and other algae.

2. Hatchery Bay, South Bass. As in No. 1, but so protected by submerged bars that *Elodea, Valisneria,* and *Potamogeton* flourish.

3. Squaw Harbor, South Bass. As in No. 2, but so protected by partially emergent bars that water-lilies and sedges grow about its somewhat mucky edges.

[1] The origin of these and the mechanical forces involved are being worked out by Prof. F. H. Krecker.

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4. Terwilliger's Pond, South Bass. Enclosed by a high bar except for a small channel. Vegetation as in No. 3, but the mucky shores well developed into a *Sparganium* and *Scirpus* marsh.

5. Hanck's Pond, Middle Bass. As in No. 4, but the bar completely closed and the shores of the pond so developed that the higher borders are grassy (see figs. 3 and 4).

6. Fox's Pond, North Bass. A marsh protected from the lake by a high gravel beach and entirely filled with muck except for a few square yards of shallow water containing *Polygonum, Myriophyllum,* etc. The central area of the marsh is covered with *Sparganium,* which gives place as one goes landward, first to sedges, then grasses, and finally to a growth of ash (see figs. 5 and 6).

FIG. 6. Fox's pond; showing the last stage in the life of a pond. The grassy edges are being invaded by grass. No dragonflies

The following species of dragonflies are found so regularly about these ponds that they may be considered as fixed items in the pond fauna:

1. *Lestes forcipatus*
2. *Lestes rectangularis*
3. *Ischnura verticalis*
4. *Enallagma carunculatum*
5. *Enallagma ebrium*
6. *Enallagma exsulans*
7. *Enallagma signatum*
8. *Anax junius*
9. *Sympetrum obtrusum*
10. *Sympetrum vicinum*
11. *Leucorrhinia intacta*
12. *Erythemis simplicicollis*
13. *Pachydiplax longipennis*
14. *Libellula luctuosa*
15. *Libellula pulchella*
16. *Plathemis lydia*
17. *Tramea lacerata*

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The following pond species appears to be strays that are not abundant, or are perhaps not seasonal from June 20 to August 1:

1. *Lestes disjunctus*
2. *Lestes unguiculatus*
3. *Lestes uncatus*
4. *Nehalennia irene*
5. *Epiaeschna heros*
6. *Aeschna constricta*
7. *Epicordulia princeps*
8. *Sympetrum rubicundulum*
9. *Libellula semifasciata*

This pond fauna shows a definite succession from the open lake fauna of such open harbors as Put-in-Bay, where no pond species occur, to the *Sympetrum-Lestes* climax in the aged ponds such as Fox's on North Bass. Perhaps this can be most easily shown by giving the Odonate fauna of the six stages of ponds just listed.

1. *Put-in-Bay.* This contains the pure lake fauna, consisting of *Argia moesta, Gomphus vastus, Neurocordulia yamaskinensis,* and *Macromia illinoiensis.*

2. *Hatchery Bay.* A mixed fauna consisting of the lake fauna as in Put-in-Bay, to which have been added the following that live in the patches of aquatic weeds: *Enallagma carunculatum* very common, *Enallagma exsulans* and *Ischnura verticalis* less common, with *Enallagma ebrium* and *Epicordulia princeps* as strays on Gibralter Island in the Bay.

3. *Squaw Harbor.* Individuals of the lake species few, but the pond species increased by the addition of *Ischnura verticalis* in numbers, with a few *Anax junius.*

4. *Terwilliger's Pond.* No lake species whatever. The following purely pond species abundant:

*Ischnura verticalis*
*Enallagma ebrium*
*Enallagma exsulans*
*Enallagma carunculatum*
*Enallagma signatum*
*Anax junius*
*Libellula luctuosa*
*Libellula pulchella*
*Tramea lacerata*

The following occasionally taken: *Lestes rectangularis, Enallagma hageni,* and *Epicordulia princeps.*

5. *Hanck's Pond.* This pond is at its richest stage as far as flora and fauna are concerned (see fig. 4). It contains all the species found in No. 4, and, because of its greater area of surrounding marsh, adds in abundance such species as:

*Lestes rectangularis*
*Lestes forcipatus*
*Sympetrum obtrusum*
*Sympetrum vicinum*
*Pachydiplax longipennis*
*Erythemis simplicicollis*
*Leucorrhinia intacta*
*Plathemis lydia*

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Fischer's Pond of Middle Bass and Smith's Pond of North Bass come in this same category.

6. *Fox's Pond.* This is no longer a pond, but a marsh with a few inches of water in some small, open places in its center. The land edges of the marsh have already become so built up that they are occupied by sedges, grasses, and trees (see figs. 5 and 6). The main area of the marsh is Sparganium, in which flourish *Sympetrum obtrusum, Sympetrum vicinum, Ischnura verticalis,* and *Lestes forcipatus* in large numbers. Occasional individuals of *Enallagma hageni, Lestes rectangularis, Lestes uncatus, Lestes unguiculatus, Anax junius,* and *Sympetrum rubicundulum* occurred among these abundant species. In the open, shallow pools of the center of the marsh a few individuals of *Aeschna* (*constricta?*), *Libellula pulchella,* and *Pachydiplax longipennis* managed to persist.

The diagram, figure 7, shows the succession of species as the open harbor ages into a pond and finally dries into a marsh. Not enough is known of the habits and life histories of these to more than suggest what the controlling factors may be. The first five species, which cling to the lake shores, demand moving water; perhaps their respiratory apparatus needs the aid of well-aerated water. These shore dwellers have either very short legs and get protection from the waves by burrowing in the lake bottom or have unusually long legs so that they can handle themselves among the wave-washed rocks. The species of *Gomphus* are the burrowers, while *Argia, Neurocordulia,* and *Macromia* are the long-legged scramblers. In the pond species *Anax* and *Aeschna* prefer vegetation with vertical stems, where the female can back down into the water to oviposit and the larvae can roost in a vertical position while lying in wait for prey. The marsh species, *Lestes* and *Sympetrum,* represented by the last six of the diagram, are adjusted to intermittent marsh conditions by the fact that they all probably pass the winter in the egg stage. *Lestes* eggs laid in the late summer and fall can dry out and then hatch with the first spring rains, probably also those of *Sympetrum.*

### 3. The Constant Pressure of the Pond Species into the Habitat of the Lake Species

Pond species remain such partly because the females prefer to oviposit in quiet water or where there is vegetation in the water. None of them oviposit with any regularity along the very extensive rocky shores of the islands. Yet there are islands in this group which possess only rocky shore lines and no vestige of ponds, but which annually yield a few individuals of strictly pond species to the collector's net. This was first noticed in the south end of South Bass, two miles from the nearest pond (Terwilliger's), where the island shores are high cliffs rising directly from the lake surface. Here *Ischnura verticalis* was common, and several *Anax junius, Epiaeschna heros,* and *Pachydiplax* were taken. *Epicordulia princeps, Libellula pulchella,* and

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*Libellula semifasciata* were seen. Ten miles to the south lay the great Sandusky Bay marshes. Undoubtedly a few of these had been blown across, but apparently the majority were the offspring of such wanderers rather than the original emigrants. The *Anax* were tenerals as well as some of the Ischnuras. These must have emerged from the near and forbidding lake shore with its waves and rocks. The most acceptable explanation is that fertile females wander from the ponds on the north side of the island or across the lake from the Sandusky marshes and manage to oviposit along the rocky shore. This could be done on calm days. Some of the young would probably survive, just enough to keep this end of the island provided with a few strictly pond species. The following small islands provide similar but more striking evidence:

*East Sister Island.* The nearest pond to this island is about seven miles south on North Bass. The shore is a coarse gravel beach, though the island is many acres in extent. Yet *Nehalennia,* the Enallagmas *ebrium* and *carunculatum, Pachydiplax* and the Sympetrums, *obtrusum, rubicundulum,* and *vicinum,* were represented on the island by a few individuals each.

*Hen Island.* This island is about twenty acres in extent with high rocky shores. The nearest pond is on North Bass, about five miles distant. On Hen Island were found a few individuals each of *Nehalennia, Lestes rectangularis, Aeschna constricta, Libellula pulchella,* and *Plathemis lydia.*

*Big Chick Island.* This is a gravel and cobble reef with the gravel piled up about ten feet high. It is perhaps an acre in extent and contains one live tree, a dozen stalks of *Scirpus,* and a few cucumber vines. It is a tern roost harboring thousands of these birds. The nearest island is a mile distant, the nearest pond about five miles. Yet an *Ischnura* and two Enallagmas were collected on the lee side of the tree in 1920. However, in 1921 none were found.

*Ballast Island.* This is a small island, perhaps ten acres in extent, but with rocky shores, and it lies one mile east of Middle Bass. Besides the usual lake species found on all the islands, *Ischnura,* the Enallagmas, *ebrium* and *exsulans,* and *Sympetrum obtrusum* were found.

*Rattle Snake Island.* This island is about a mile long, but is surrounded on all sides by precipitous limestone cliffs. The nearest pond is at least two miles east of it. On it were caught in 1920 a female *Enallagma* and a *Pachydiplax.*

*Sugar Island.* This is about a quarter of a mile long, is low, but has clean, rocky shores, the eastern end being sandy and a great place for *Gomphus.* In one spot low enough to be continuously renewed by seepage from the lake was a small puddle not over ten feet long and three wide. In its neighborhood were taken *Ischnura,* the Enallagmas, *ebrium* and *carunculatum, Anax, Pachydiplax* and the Libellulas, *luctuosa,* and *pulchella.* This

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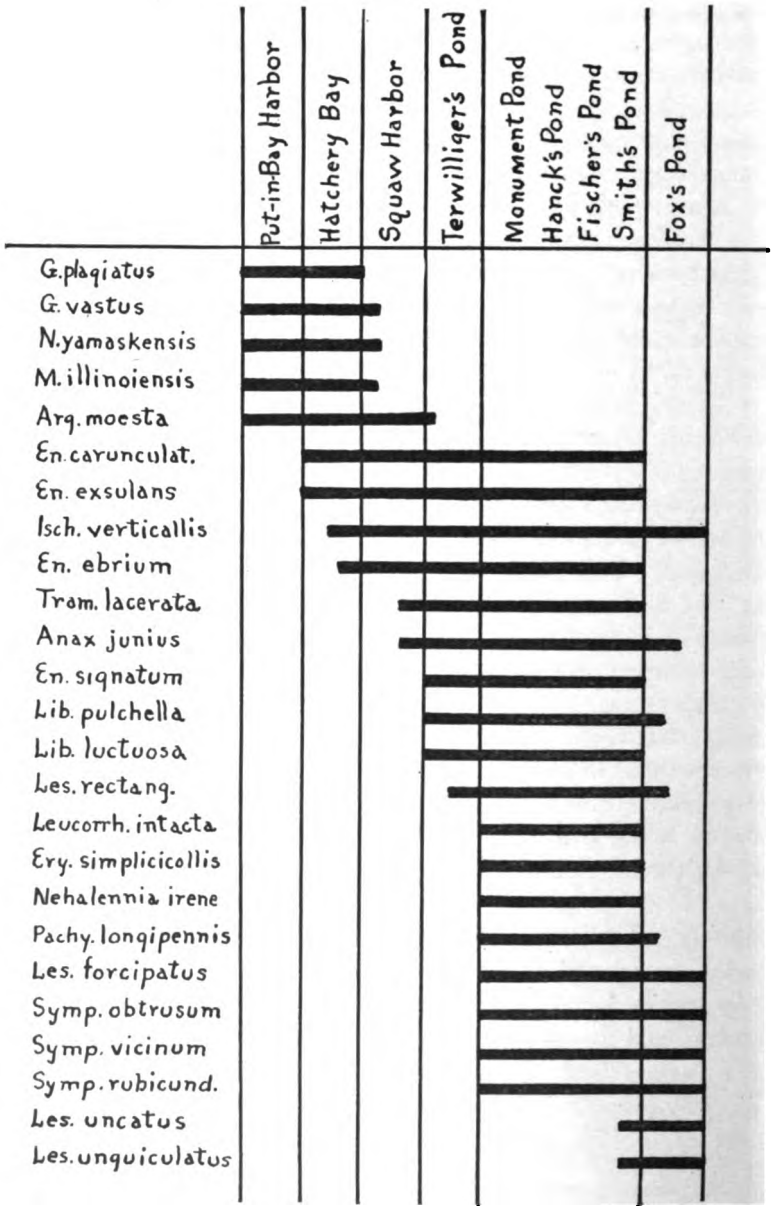


FIG. 7. The succession of dragonfly species as the ponds develop and then age

shows how even the smallest of suitable waters are sought out. The nearest pond was nearly a mile distant on Middle Bass.

It is interesting to note that the lake species are all put by systematists low down in Odonate phylogeny, while the majority of the larger pond species

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are in the *Libellulinae,* which is the latest and highest of the subfamilies of dragonflies. This means that the lake species are specialized remnants of a preceding fauna, of which the pond species have been already largely displaced by the very modern *Libellulinae.* Ponds are the most acceptable Odonate habitat because of their quiet waters and abundance of dragonfly food, so the later and better forms of Odonata supplant the more primitive species about ponds first.

In more detail: the three Gomphines are exceedingly specialized in the burrowing habit of the larvae, which protects them from the currents and the waves, in the protective coloration of the adults, and in the spatulate abdomen of the latter, which enables them to dodge easily along narrow streams. These are members of the family *Aeschnidae,* which reached its climax before or in early Tertiary times. *Neurocordulia* and *Macromia* are specialized in their long-legged, spider-like larvae that can maintain themselves among the wave-washed rocks, also in the crepuscular habits and cryptic coloration of the former, and in the great wing speed of the latter, which is one of the swiftest dragonflies. These are both in the subfamily *Cordulinae,* a primitive and almost extinct branch of the *Libellulidae,* from which the present dominant *Libellulinae* have probably developed. *Argia* is a remnant of a small group of damselflies that probably reached their climax in the Eocene. For a damselfly its larvae have long legs, while its adults oviposit in wet drift. These all have a long life history of from one to three years.

The pond *Libellulinae* have a life history never longer than one year, and in some species only three months. They are very active hunters and in this short, fast life outlive the specialized, older, and slower *Aeschnidae* and *Cordulinae* of the lake shores. It is interesting that two *Aeschnidae, Anax,* and *Aeschna constricta,* still hang on in the ponds in competition with the *Libellulinae. Anax* has speeded up its life cycle to three months, while *Aeschna constricta,* which is the most widely spread species of a genus which has a dozen species that still persist about the ponds and streams on the northern edge of the main range of the *Libellulinae,* has a nymph that is the last word in savage voraciousness. The *Libellulinae* have probably originated about the ponds of the tropics, where the subfamily is wonderfully rich in pond forms, but there they have already begun to develop specialized stream species. Apparently they are spreading as pond species into the temperate zones, but have not occupied these long enough to have developed a series of specialized stream species there. Curiously enough, some of the more specialized stream *Libellulinae* of the tropics resemble the stream-inhabiting Gomphines of the north in the burrowing habits of their larvae and the spatulate abdomen of the adult. The *Libellulinae* simply outlive the *Aeschnidae* and the *Cordulinae.* Their larvae are generalized so that they are well off on a mud bottom, in trash, or amongst vegetation.

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The pond damselflies are all high in the phylogeny of that group as compared to the low position of the lake shore *Argia moesta*. So their case is parallel to that of the dragonflies.

The marsh species, the Sympetrums and the Lestes, are again specialized. They each have one brood a year, and the Lestes, and probably also the Sympetrums, pass the winter in the egg stage. Lestes oviposits in the late summer or fall and the eggs hatch with the first spring rains. This adjusts them to marshes that have a habit of drying out in the fall of the year. While many other species may hang about a marsh during a series of wet years, a single dry fall must wipe out such unadapted species.

Our data cited above indicate that already these modern *Libellulinae* are crowding into the habitat of the lake species, while there is no data to indicate that the lake species are crowding similarly into the ponds. Our data show also that these particular pond species probably will never successfully colonize the lake shores. As in the tropics, the lake shores will eventually be colonized by specialized *Libellulinae*.

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# REVIEWS

## The New Meteorology[1]

A war story relates that a commanding officer ordered his Adjutant to ascertain the probable direction of the wind at a specified hour on the following day. "Can't tell you offhand, sir," replied the Adjutant. "I'll send out a detachment to catch a couple of Boches—quickest way, sir." It might be difficult to provide a voucher for the foregoing, but it illustrates an important and embarrassing discovery made by American officers overseas, namely, that the Germans were abundantly provided with all the necessary meteorological information of which they themselves were almost hopelessly destitute. "Back in the high school," said a youthful shavetail, "I learned that water froze at 32°; but here in this bloomin' country it doesn't freeze till the weather gets down to zero!"

One of the first and most necessary steps, therefore, was the training of a corps of officers and men in the elements of aerology, or meteorology in its broader sense. For this purpose the United States Weather Bureau detailed members of its staff as instructors and field officers. Among them was Professor Alexander McAdie, at that time in charge of the Blue Hill Observatory. His appointment as senior aerographic officer overseas indicates his qualifications as a meteorologist.

McAdie's Principles of Aërography, published in 1917 and followed recently by a new edition, is one of the first, if not the first, publication which may be regarded as an exposition of the new meteorology. Just as the school geography of calico maps and lists of localities to be "bounded" has expanded into the science of environment as the dominating factor in human activities, so the new meteorology has expanded and developed into a science that is the full partner of the new geography. It is the science of the air and its conditions as they govern life; for, after all, human history may be regarded very largely as a quantitative expression of temperature, wind, and rainfall.

Weather conditions of the most densely peopled part of the United States may be the result of air pressure in polar regions, to be learned at the Greenland weather station. And the ice which blocks the harbor of Halifax may be born of wind and weather in the Caribbean Sea. Rainfall in India may determine the price of wheat in Chicago; and the height of water in the Nile may mean either prosperity or adversity to the cotton planter in Texas. Not air measurements at ground level, but air measurements a score of miles above ground level, determine the winter's consumption of coal; and, incidentally, whether humanity is to have happiness or misery for its side partner during

[1] McAdie, Alexander, "The Principles of Aërography," Rand McNally and Co., Chicago–New York, 1921.



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a coming winter. "Air to be warmed must first be cooled; and air to be cooled must first be warmed," Dr. Humphreys tells us; and this is Dame Nature's method of regulating things. McAdie's Aërography—he might as logically have styled the book Aërology—presents the new meteorology in this light.

The chapter, Stratosphere and Troposphere, is presented not only with diagrams and tabulated matter necessary for reference, but also with a clear and interesting descriptive text—apparently the first treatise in the United States to contain an exposition of this feature of meteorology. The subjects of atmospheric water vapor, winds, clouds, and condensation are splendidly illustrated. The cloud photographs, a few by Ellerman and Ziel, but mainly those made by the author, are fine pieces of work—as artistic as they are interesting. The cirrostratus storm-breeder, with its wispy edges, would be a most useful print as a part of the equipment of the cooperative observer's station.

The chapter on atmospheric electricity contains Simpson's theory of thunderstorms which has been pretty well substantiated by artificial reproduction of atmospheric discharges. It is interesting to note in this connection that a rod of electrified vulcanite brought near a fine spray discharged from a nozzle causes the droplets to coalesce into tremendously large drops as they fall. The author brings out the important fact that thunderstorms and tornadoes are due to the same abnormal movements of the air; they are in the same class. The chapter is illustrated by a dozen photographs of lightning flashes, spectra, and graphs.

Professor McAdie arouses the suspicion that he is a dreadful crank on the subject of the metric system. So far as C.G.S. units are concerned his attitude is justifiable, for, in time, these are the terms in which the physics of the air must be mathematically expressed. Temperature is expressed in the degrees of the absolute scale. But inasmuch as air temperatures are expressed in Fahrenheit degrees among English-speaking people, the author would have simplified matters by placing them parenthetically in the text.

Professor McAdie's Aërography is a treatise rather than a textbook. Nevertheless the student in meteorology who fails to use it along with his textbook misses a lot of instructive literature of the subject. It is written in good, clear English and is interesting from cover to cover. The author evidently is not in sympathy with the opinion that a treatise to be scholarly must be in a style so stupid as to be lethal.

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## TUTIRA[1]

Anyone who appreciates a narrative of energy, persistence, and indomitable struggle against seemingly insuperable difficulties will enjoy this stirring history of Tutira, a sheep station of about 100 square miles in the North Island. The ecologist especially will find in it a graphic account of the vegetation before settlement 49 years ago, of the immigration of an alien flora and fauna, and of the great changes which have ensued under the influence of man and sheep. Almost half of the book is strictly ecological, a small portion is devoted to physiography and geology, and the balance to the history of the station.

The author modestly disclaims scientific erudition, but a perusal of the book proves that he is not only an ecologist, but an observer of remarkable discrimination who has had unusual opportunities to see ecological processes at work and has faithfully recorded facts for forty years. He has the dynamic viewpoint to a degree: with him plants and animals are continually increasing or decreasing in numbers, immigrating or disappearing, dominating or sinking into insignificance, as environmental factors change. We all *believe* in succession, but none of us actually *sees* much of it. The author, however, has seen stage after stage pass on his own land, and understands the cause of each. To be sure, succession in Tutira has been hurried by the action of man, but the essential processes remain the same.

In prehistoric times the land was covered by a heavy podocarp forest. Some trees still remained in 1882, but most were represented only by fallen or buried logs. The removal of the trees is attributed to fires started by the Maoris within the last four centuries. When the author first settled on the station, less than 3 percent of its area was forested, smaller amounts were in flax (*Phormium*) and cat-tail, and the balance was a vast sea of bracken fern. The subjugation of the bracken was carried on through crushing by sheep, followed by burning; and attempts were made to naturalize various forage plants by broadcast sowing after the fires. The latter was not successful, and the repeated fires led to an extraordinary development of manuka (*Leptospermum scoparium*), which soon became more troublesome than the bracken had been previously. It was finally subdued by changing the annual burning from fall to spring, and with its suppression came a great development of the native grasses *Microlaena stipoides* and *Danthonia semiannularis,* which remain the most important forage plants today.

While almost 250 alien plants have appeared at Tutira, most of them are confined to the neighborhood of houses, roadsides, gardens, and the like, and show little or no ability to compete with the native vegetation. Alien grasses, even when encouraged, have not become important for forage. This condi-

[1] Guthrie-Smith, H., "Tutira, the Story of a New Zealand Sheep Station." Pp. xxi + 400. 22 plates, 127 text figures, 16 maps. William Blackwood and Sons, Edinburgh and London, 1921. 42 shillings.

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tion is, of course, essentially like the behavior of alien plants in America, but just the contrary of what we have always believed of New Zealand since the early statements of Hooker. Only one alien plant, the blackberry (*Rubus fruticosus*), has become dangerous to the sheep industry. For practically every one of these aliens the author can record the year and place of its first appearance and the details of its further history. For most of them he knows the exact means by which they reached the station, and for the alien animals also the migration route followed.

All these facts are presented readably, without attempts at theorization, and the whole book is a mine of ecological information.

H. A. GLEASON

NEW YORK BOTANICAL GARDEN

## STREAM POLLUTION[1]

This paper is a valuable contribution to the literature of stream pollution. The subject is treated in general and the results will be found applicable to any body of water. The subject matter is treated under such headings as Polluting Materials, Fish Requirements, Zone of Recent Pollution, Septic Zone, Zone of Recovery, Clean Water Forms, Tolerant Forms. Figures are given of the various types of animal and plant life that is characteristic of different degrees of pollution. There is a good but not exhaustive list of references.

The reviewer takes exception to some of the molluscan types cited (plate IV). Goniobasis and Campeloma are not, as a rule, tolerant forms, although they may be found in slightly polluted waters, as may many other types of animals. The little clam Pisidium is usually an inhabitant of clean water and is by no means tolerant. The Pulmoniferous water snails are very tolerant because they take free air. We believe that the fresh-water mussels are good indicators of degrees of pollution, and when they cease to be present in a stream normally fitted for them the pollution may be deemed to be bad. Bottom-inhabiting animals normally inhabiting clean water are good indicators, because they can not get away and must become tolerant or perish. Recent studies in an Illinois stream, covering a distance of nearly 50 miles, in which the sewage of two cities is emptied, indicated clearly that both naiads and crawfish were notably affected by these conditions, the naiads being the less tolerant.

In another place[2] the reviewer presented a study of the Genesee River, at Rochester, N. Y., a heavily polluted stream, showing that the water-breathing snails were the first to give out, not being tolerant, and the air breathers were quite tolerant, in fact remaining until the water was the consistency of dish water before being driven out.

[1] Suter, Russel and Emmeline Moore, "Stream Pollution Studies." State of New York, Conservation Commission, 1922, pp. 1–34, many figures.

[2] American Naturalist, LIV, pp. 152–161, 1920.

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On page 7 of the paper here reviewed the statement is made that "Snails, black fly larvae, water boatmen, and similar forms have a wide range and therefore are not good guides to water condition, except to the scientist who can distinguish between the different species of these animals." Certainly, this is true, and the statement indicates that such studies should not be carried on without the aid of some of these trained scientists who are usually willing to aid in the identification of such material. It is highly important that we should know just which species are tolerant and which are not, for one species of a genus may be highly tolerant and another not the least so. There is no department of public work in which careful and exact studies need to be made more than in the study of stream pollution and the effect on different kinds of animal life.

The paper by Suter and Moore is in the right direction and we hope they will carry on the work in different streams to ascertain the exact state of affairs under different conditions.

FRANK C. BAKER

UNIVERSITY OF ILLINOIS

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# ZOOLOGICAL ABSTRACTS

**Baker, H. B.** The Mollusca collected by the University of Michigan—Walker Expedition in Southern Vera Cruz, Mexico. I. *Occasional Papers, Mus. of Zool., Univ. of Mich.*, No. 106. 1–94, 17 plates, Feb. 1922.

A very interesting paper in which the ecological features of the region are outlined and classified according to the method of Ruthven in papers from this region. Lowland forest, lowland forest clearings, savannah forests and thickets, and savannah grassland constitute the land habitats. Lowland forest ponds, savannah ponds, sluggish and rapid rivers, and lake (laguna) make up the water habitats. The species are arranged systematically, some ecological information being given under each. Both the systematic and ecological work is well done and the paper is a very valuable addition to the literature of Mexican Mollusca. F. C. BAKER.

**Campbell, V. A., D. Hargood-Ash, and Leonard Hill.** The effect of the cooling power of the atmosphere on body metabolism. *J. Physiol., London*, 55: 259–264. 1921.

Experiments on man are recorded, indicating that the basal metabolism of the body cells is raised by cool out-of-door conditions, and that shivering is not necessary to raise metabolism. L. R. DICE.

**Eigenmann, Carl H., and William Ray Allen.** A leaf mimicking fish. *Biol. Bull.* 41, 301–305, figs. 1–3, 1921. On the basis of observations in South America, of the native name for the fish, and of its structure and coloration as determined in the laboratory, the authors conclude that the fishes of the genus *Monocirrhus* are leaf-mimicking. CARL L. HUBBS.

**Grier, N. M.** Final Report on the Study and Appraisal of Mussel Resources in selected Areas of the Upper Mississippi River. *American Midland Naturalist*, 1–33, Jan. 1922.

This paper describes the local conditions of bottom and shore for a stretch of the Mississippi River about 85 miles in length, above and below Lake Pepin. The effect of dams and other modifications are noted, as well as the relative abundance of the different species of mussels. While undertaken from the standpoint of commerce, the paper contains much of interest to the ecologist. F. C. BAKER.

**Hartridge, H.** The avoidance of objects by bats in their flight. *J. Physiol.*, 54: 54–57. 1920.

Suggests that a bat during flight emits a note of short wave-length and that this sound is reflected from objects in the vicinity, forming sharp sound reflections, which the bat is able to discriminate with its acute hearing. The animal is thus able to detect and avoid objects while it is flying in complete darkness. L. R. DICE.

**Howe, R. Heber, Jr.** The distribution of New England Odonata. *Proc. Boston Soc. Nat. Hist.*, 36: 105–133. 1921.

A general discussion of the factors affecting the distribution of New England Odonata: Physiography, air temperature and moisture, wind, water temperature, salinity, ecologic station, etc. Howe thinks that to attempt to define too closely and arbitrarily life zone boundaries is to confuse rather than to elucidate the problems of distribution. He considers it best to recognize only Austral and Boreal elements in the New England fauna, and thinks that the recognition of the Transition zone is

[1] Reprints of Zoological Abstracts, printed on one side for pasting on cards, may be secured from the Business Manager of ECOLOGY, Brooklyn Botanic Garden, for twenty-five cents per volume of four issues.



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illogical. However, he states that the Alleghenian and Carolinian faunal areas are easily recognized, and he also recognizes a Maritime District in New England. L. R. DICE.

**Hubbs, Carl L.** Geographical variation of *Notemigonus crysoleucas*—an American minnow. *Trans. Illinois St. Acad. Sci.*, 11: 147–151. 1921.

An increase in the number of anal rays from northwest to southeast is demonstrated. The variations are not correlated as usual with stream systems, perhaps rather with temperature. A dwarfing due apparently to unfavorable conditions is noted and is considered an instance of the great adaptibility of the species. T. L. HANKINSON.

**Järvi, T. H.** Die kleine Maräne *Coregonus albula* L. im Deitelesee. Eine ökologische und ökonomische Studie. *Ann. Acad. Sci. Fennicae*, ser. A, 14: 1–301, many figures and maps, 1920. A very extensive study of the ecology, life-history and economics of a European fish related to our lake-herring (*Leucichthys*). The fish discussed is a typical plankton feeder; it usually lives in the deeper parts of the lake, but in early summer lives in shallow water; it makes diurnal vertical movements. Spawning occurs in the fall, the time being controlled by the water temperature (7° to 6° C.). Its enemies and parasites are mentioned. Its growth, which is slow, is discussed at length; the age determinations were made by the scale method. The same paper was published in Swedish in 1919, under the title: Siklojan i Finska Sgöar. I. Keitele (Finlands Fiskerier, Bd. 5). CARL L. HUBBS.

**Moore, J. Percy.** Use of fishes for control of mosquitoes in northern fresh waters of the United States. App. 4, *Rept. U. S. Comm. Fish. for 1922.* (Bur. Fish. Doc, No. 923): 1–60. 1922. A general consideration of the biological control of mosquitoes, with particular reference to fish enemies. Field experiments coupled with food studies indicate the relative value of different fishes in different situations. CARL L. HUBBS.

**Needham, James G., Chancey Juday, Emmeline Moore, Charles K. Sibley, and John W. Titcomb.** A biological survey of Lake George, N. Y. *State of New York, Conservation Commission*, 1922; 78 pp.; 27 figs. A comprehensive study of Lake George, undertaken in 1920 for the purpose of determining the most practical methods of increasing fish production. The recommendations are made both by Needham and Titcomb, and seem wise to the reviewer. Needham discusses the hydrography and the benthic and planktonic vegetation, and gives a general and somewhat popular account of the turn-overs of the lake's vegetation into fish food, finally recommending further studies in the fishery biology of inland lakes. He stresses the need of an experimental hatchery. Juday gives the results of his investigations into the distribution of temperatures, light, dissolved oxygen and carbon dioxide and plankton throughout the lake, and of the organisms on the bottom. Moore traces back to primary sources the food supply of a number of the important fishes of the lake. Sibley has an annotated list of the fishes of the lake, and a rather brief account of the food of the adult game fishes, Moore having studied the young fishes chiefly. Titcomb concludes the paper with an article on fish cultural observations.

Lake George is over thirty miles long and rather narrow. A small part of the bottom, in three isolated areas, is over 100 feet deep; the maximum depth recorded is 175 feet. The water is unusually clear; attached green plants grow to depths of at least 50 feet, and plankton algae are abundant at three times this depth. The nannoplankton was found to be over forty times greater (by weight) than the net plankton; *Aphanocapsa delicatissima* was its chief element. The chief vegetation areas are the "weed beds," chiefly Potamogetons; the "grass beds" of Nitella, at depths of 22 to 45 feet, and finally the "moss beds" in still deeper water. The plant beds are very productive of fish food, the free and attached plants and plant fragments supporting an abundant growth of invertebrates, chiefly eaten by the fishes. In the open water, the food chain comprises phytoplankton, entomostracans, white-fish (*Leuc-*

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*ichthys*), lake trout. The final element of this chain is considered the most important fish of the lake. CARL L. HUBBS.

**Osborne, W. A.** Physiological factors in the development of an Australian race. *Med. J. Australia,* 1920 v. 2: 261–267. 1920.

A discussion of the factors concerned in the establishment of a permanent white race in Australia. Race, food, disease, and climate are considered. The rearing of healthy children is of course the greatest difficulty. L. R. DICE.

**Pellegrin, Jacques.** Les poissons des eaux douces de l'Afrique du Nord francaise Maroc Algerie, Tunisie, Sahara. *Mem. Soc. Sci. nat. Maroc,* 1, No. 2, 1–216, 1921. This paper contains a general discussion of the geographical distribution of fresh-water fishes, with particular reference to Africa. The regions and subregions recognized are named and mapped. The northeastern portion of Africa, north of the Sahara, is discussed in detail, and designated the Mauritanic subregion of the Palearctic region. The African, Ethiopian or Equatorial Cyprinoid region is divded into seven subregions. Of further interest to ecologists are the author's discussions of the fishes of brackish, thermal, mineral, subterranean and desert waters. The 54 forms of fishes known from the area under discussion are all described and figured. CARL L. HUBBS.

**Richardson, R. E.** Changes in the bottom and shore fauna of the middle Illinois River and its connecting lakes since 1913–1915 as a result of the increase, southward, of sewage pollution. *Bul. Ill. Nat. Hist. Survey,* 14: 33–75. 1921.

Marked changes in the bottom fauna were noted in this portion of the river as a result of the sewage contamination. Many intolerant forms were totally obliterated, while pollution and tolerant forms had invaded these areas. C. JUDAY.

**Suter, Russell, and Emmeline Moore.** Stream pollution studies. *State of New York, Conservation Commission.* Pp. 1–27, pls. 1–7. 1922. Organisms are considered, and recommended for practical use, as indicators of the intensity of stream pollution. The zone of recent pollution is characterized by sewage fungi, and near its lower limits by Tubifex; this leads into the septic zone, characterized by absence of algae and by the presence of certain insect larvae, notably *Eristalis.* The zone of recovery is marked by the abundance of bloodworms and the reestablishment of green plants. The energy and food relations of animals and plants in general, and specifically in relation to the zones of pollution, are briefly but well summarized. Figures of pollution, tolerant and clean-water organisms are given. Published data on the limits of tolerance of fishes to trade wastes are tabulated. CARL L. HUBBS.

**Tiffany, Lewis Hanford.** Algal food of the young gizzard shad. *Ohio Jour. Sci.,* 21, 113–122, 1921. This fish (*Dorosoma cepedianum*) is a plankton feeder. The gill rakers form an efficient sieve. Algae of many species predominate in the stomach contents, animals amounting to 0 to 30 percent only. Mud is taken only incidentally. The fish is important in that it holds a position as a direct connection between microscopic algae—the ultimate fish food—and the game fishes. CARL L. HUBBS.

**Weymouth, Frank W.** The Edible Clams, Mussels and Scallops of California. *Bull. 4, Fish and Game Comm., California,* pp. 1–72, 19 plates, 1920.

This paper is an attempt to estimate the economic importance of the shell fish industry and resources of California. It is based on a systematic plan, the species being arranged in more or less exact taxonomic relation to each other. There is an excellent key to the species which will be of use to those not versed in the mysteries of modern classifications.

The response of species to the physical environment is rather graphically brought out in a study of the clams of Anaheim Slough, where the different kinds of shellfish are described as burrowers, borers, fixed, and active animals. The dependence of animals on favorable habitats for development is brought out. About 50 pages are

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devoted to a description of the edible bivalves of California, and we believe this is one of the best attempts in this direction. Habitats and habits are given for each species, and some very interesting ecological notes are appended.

While the methods employed in this paper are somewhat different from those used in more technical ecological papers, there is, nevertheless, a vast amount of ecological information which the ecologist may use with profit. The illustrations are on the whole very good, several being the best seen of marine bivalves. FRANK C. BAKER.

**Winslow, Mina L.** Mollusca of North Dakota. *Mus. Zool., Univ. Mich., Occ. Papers,* No. 98. 18 pp. 1921.

A valuable paper on the Mollusca of this little-known region. Ecological notes are given concerning the character of the different lakes, several of which are so strongly alkaline as to be wholly or partially devoid of molluscan life. Forty-eight species of fresh water mollusks are enumerated, many of which are accompanied by ecological notes. There is a good bibliography of the literature relating to North Dakota Mollusca. F. C. BAKER.

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# NOTES AND COMMENT

## NOTE ON SPECIFIC ACIDITY

The relative merits of an exponential method of statement of acidity beginning at a theoretical normality point, and of a direct method beginning at neutrality, have been discussed by several writers (see 'literature'), and it is not intended to continue the controversy here. Many scientists will always prefer the one because of its theoretical significance, while some will favor the other because of its greater ease of comprehension. Specific acidity, the term used in the direct method, is the amount of active acid (*i.e.*, hydrogen-ion) present in a liter of a given solution, expressed in terms of the approximate hydrogen-ion concentration of pure water (0.000,000,1 gram per liter) as a unit; specific alkalinity is the corresponding amount in terms of hydroxyl-ion.

One of the objections which has been raised to the use of the conceptions of specific acidity and specific alkalinity is that the continuity in the acid-base system of equilibria is thereby lost sight of. (Clark, Atkins). It is here desired to point out that this continuity can be preserved without resorting to a logarithmic form of statement, merely by replacing specific alkalinities by their reciprocals, which are the corresponding specific acidities. The recent attempt of Adamson to preserve the continuity by considering specific alkalinities equivalent to negative specific acidities represents a misunderstanding of the significance of the terms.

TABLE I. $P_{\bar{H}}$—*Specific acidity equivalents*

| PH | Specific Acidity | PH | Specific Acidity | Specific Alkalinity |
|---|---|---|---|---|
| 4.0 | 1,000 | 7.0 | 1.0 | 1 |
| .1 | 800 | .1 | 0.8 | 1.25 |
| .2 | 630 | .2 | 0.63 | 1.6 |
| .3 | 500 | .3 | 0.5 | 2 |
| .4 | 400 | .4 | 0.4 | 2.5 |
| .5 | 315 | .5 | 0.32 | 3.15 |
| .6 | 250 | .6 | 0.25 | 4 |
| .7 | 200 | .7 | 0.2 | 5 |
| .8 | 160 | .8 | 0.16 | 6.3 |
| .9 | 125 | .9 | 0.13 | 8 |
| 5.0 | 100 | 8.0 | 0.10 | 10 |
| .1 | 80 | .1 | 0.08 | 12.5 |
| .2 | 63 | .2 | 0.063 | 16 |
| .3 | 50 | .3 | 0.05 | 20 |
| .4 | 40 | .4 | 0.04 | 25 |
| .5 | 31.5 | .5 | 0.032 | 31.5 |
| .6 | 25 | .6 | 0.025 | 40 |
| .7 | 20 | .7 | 0.02 | 50 |
| .8 | 16 | .8 | 0.016 | 63 |
| .9 | 12.5 | .9 | 0.013 | 80 |
| 6.0 | 10 | 9.0 | 0.010 | 100 |
| .1 | 8 | .1 | 0.008 | 125 |
| .2 | 6.3 | .2 | 0.0063 | 160 |
| .3 | 5 | .3 | 0.005 | 200 |
| .4 | 4 | .4 | 0.004 | 250 |
| .5 | 3.15 | .5 | 0.0032 | 315 |
| .6 | 2.5 | .6 | 0.0025 | 400 |
| .7 | 2 | .7 | 0.002 | 500 |
| .8 | 1.6 | .8 | 0.0016 | 630 |
| .9 | 1.25 | .9 | 0.0013 | 800 |
| 7.0 | 1 | 10.0 | 0.0010 | 1,000 |



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For translating $P_H$ values which appear in the literature into specific values, so that the relative magnitudes represented can be grasped, the writer keeps at hand a table, which seems likely to be of sufficient interest to others to justify its publication here. In the portion of the table where $P_H$ is greater than 7 (alkaline reactions) those desiring continuity may use the values in the specific acidity column; while those who prefer to think of such solutions as alkaline may use the values in the one so headed.

LITERATURE

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WASHINGTON, D.C. EDGAR T. WHERRY

EXTREMELY DIVERSIFIED HABITAT OF A MARINE GASTROPOD

While on the University of California Alaska Expedition in 1907 Mrs. Kate Stephens of the San Diego Society of Natural History made a collection of *Buccinum glaciale* Linnaeus in Glacier Bay. This body of water is greatly freshened through the discharge into it of large quantities of glacial ice. For the same reason the waters are chilled almost to the freezing point. The mollusks were found where there was no sea weed, and the bottom was of soft mud with the exception of the small rock upon which they were living.

Shortly afterwards the same species was found living in Bear Bay, Peril Strait. The ocean water here is relatively warm and received directly from the Japanese current. Sea weeds were growing luxuriantly.

Many marine mollusks are very susceptible to changes in salinity and temperature, and this is so notable an exception that it seems worthy of record. The shells of the animals from the two localities are about the same size and the same series of variations may be seen in each lot.

CALIFORNIA ACADEMY OF SCIENCES G. DALLAS HANNA

EARTHWORMS AND SOIL REACTION

In an interesting experiment on the influence of soil reaction on earthworms Arrhenius[1] shows that, while these animals live and propagate in a soil having a reaction of $P_H$ 6, they cannot live at a $P_H$ of 5. In the course of soil tests on Mt. Desert Island, Maine, with the Wherry method[2] vigorous earthworms were found

[1] Arrhenius O. "Influence of Soil Reaction on Earthworms." Ecology II: 255–257, 1921. See especially the table on p. 257.

[2] Wherry E. T. "Soil Acidity and a Field Method for Its Measurement." Ecology I: 160–173, 1920.

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in a soil which had a reaction of $P_H$ 5.5 (specific acidity of 30 by the Wherry scale). It will be noted that this falls exactly in between the columns given by Arrhenius (loc. cit. p. 257); at $P_H$ 5 his earthworms were all dead at the end of 3½ days, while at $P_H$ 6 they were all living.

BARRINGTON MOORE

### ASSOCIATION FOR ANTHROPO-ECOLOGICAL RESEARCH [1]

An association for anthropo-ecological research has been founded recently at the University of Vienna, under the auspices of Dr. Julius Spinner and Dr. Ferd. Scheminzky, the latter having undertaken the organization of the physical-biological group, and the former that of the psychological and sociological group. The aim of the association is the thorough investigation of the dependence of the mental and physical character of the individual and of social groups and cultures on environmental conditions. The cooperation of a considerable number of investigators has already been assured, and the results will appear as single contributions or as compilations. The foundation of an institute for anthropo-ecological research is also planned. The association requests all other scientific societies and investigators working in the same field to make known the character and extent of the work already done or under way, in order that useless duplication of effort may be avoided, and that contributions already published be made available. Communications should be addressed:

An die Arbeitsgemeinschaft für anthropo-ökologische Forschung,
Wien, I., Universität, Austria.

[1] Wiener Mediz. Wochenschr., 1922, No. 19.

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